

## Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Dictyonellidae

BELINDA ALVAREZ<sup>1</sup> and JOHN N.A. HOOPER<sup>2</sup>

<sup>1</sup>Museum and Art Gallery of the Northern Territory, GPO Box 4646, Darwin NT 0810, AUSTRALIA

belinda.glasby@nt.gov.au

<sup>2</sup>Queensland Museum, PO Box 3300, South Brisbane QLD 4101, AUSTRALIA

jolnh@qm.qld.gov.au

### ABSTRACT

Eight species in five genera of the family Dictyonellidae, including one new species (*Dictyonella chlorophyllacea* sp. nov.), are recorded for northern Australia as part of a revision of the order Halichondrida in this region. The genera *Dictyonella*, *Phakettia* and *Scopalina* represent new records for the region. *Dictyonella sensu stricto* and *Phakettia* have not been recorded in Australian waters previously. All the species reported here are common throughout northern Australia and are more widely distributed in the Indo-Pacific Ocean. Descriptions and discussion of those species are presented here. Lectotypes for *Acanthella carteri* Dendy, 1889 and *A. aurantiaca* Keller, 1889 are designated.

### INTRODUCTION

The family Dictyonellidae was revised by Van Soest *et al.* (2002). It is a relatively new family erected within the order Halichondrida to receive a group of genera included in the polyphyletic former order Axinellida (Van Soest *et al.* 1990; Van Soest 1991). It currently includes 10 genera and approximately 86 species segregated amongst the genera as follows: *Acanthella* (30 species); *Dictyonella* (12 species); *Liosina* (3 species); *Lipastrothethya* (4 species); *Phakettia* (5 species); *Rhaphoxya* (8 species); *Scopalina* (12 species); *Stylissa* (14 species); *Svenzea* (5 species); *Tethyspira* (1 species) (Van Soest *et al.* 2008). The species of this family are characterised by the lack of an ectosomal skeleton, a fleshy or 'cartilaginous' appearance and a dendritic-halichondroid choanosomal skeleton composed mainly of styles, but complemented with oxeas and/or strongyles in several species.

Some dictyonellid genera such as *Acanthella* and *Stylissa* include polyphyletic assemblages of species, which compromises the integrity of the family as a monophyletic taxon. Based on the definitions given in *Systema Porifera* (Hooper & Van Soest 2002), species of *Acanthella*, formerly a genus of the Axinellidae, have been consistently mistaken for the axinellid genus *Phakellia* (e.g. *Phakellia dendyi* Bergquist) and vice-versa (e.g. *Phakellia cavernosa* (Dendy)). Equally, species of *Stylissa* have been mistaken for *Anletta* (e.g. *Auletta constricta* Pulitzer & Finali), *Axinella* (e.g. *Axinella carteri* (Dendy), *A. massa* Carter), *Phakellia* (e.g. *Phakellia connulosa* Dendy), *Acanthella* (e.g. *Acanthella inflexa* Pulitzer and Finali), and with the halichondrid genus *Hymeniacion* (e.g. *Hymeniacion connulosa*). The taxonomic confusion among these genera is one of the reasons for the long-lasting debate regarding

the monophyly of Halichondrida and its families, including Dictyonellidae (see Alvarez *et al.* 2000; Erpenbeck *et al.* 2005b; Erpenbeck & Van Soest 2005; Erpenbeck *et al.* 2006). Phylogenetic studies based on molecular data also showed the family as non-monophyletic (e.g. Alvarez *et al.* 2000; Erpenbeck *et al.* 2005a, 2005b, 2006). Regional taxonomic revisions have an important role for the understanding and definition of these groups of genera which are characterised by very few and apparently simplistic characters, and which include species with a high degree of morphological variability, and such revisions are expected to produce additional knowledge to clarify the classification of Halichondrida.

The present paper represents the second contribution of the revision of the order Halichondrida in the northern Australian region, and it includes only the family Dictyonellidae. Alvarez & Hooper (2009) have already provided a detailed and extended introduction to the order and the family Axinellidae. Revision of the two remaining families represented in the region, Halichondriidae and Heteroxyidae, will follow in subsequent papers.

### MATERIALS AND METHODS

This revision is restricted to material of Dictyonellidae from the tropical northern Australian waters of the Northern Territory and Queensland coast, from the Admiralty Gulf in the west to Torres Strait in the east, approximately between 125° E and 142° E (Alvarez & Hooper 2009; Fig. 1). It does not extend into the species-rich areas of the Great Barrier Reef or the Northwest Shelf of the northeastern and northwestern Australian coasts, respectively. These regions are the subjects of future studies on their poriferan faunas.

Complete locality and collection data for non-type voucher material deposited at the Queensland Museum and the Museum and Art Gallery of the Northern Territory are listed in the Appendix. The distribution of species is given according to the marine provinces defined by Spalding *et al.* (2007). Measurements of spicules are based on 25 spicules (unless indicated in square brackets) and denoted as range (and mean  $\pm$  1 S.E.) of spicule length and width. All other methods are as presented in Alvarez & Hooper (2009).

#### ABBREVIATIONS

Abbreviations used in the present paper are: AIMS, Australian Institute of Marine Sciences; BMNH, Natural History Museum, London (formerly British Museum (Natural History)); CRRF, Coral Reef Research Foundation, Palau; GBR, Great Barrier Reef, Queensland, Australia; MAGNT/NTM, Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin; NT, Northern Territory, Australia; MNHN, Muséum national de Histoire Naturelle, Paris, France; MSNG, Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy; SMF, Senckenberg Research Institute and Natural History Museum, Frankfurt; QLD, Queensland, Australia; QM, Queensland Museum, Brisbane; WA, Western Australia, Australia; ZMA, Zoologisch Museum, University of Amsterdam; ZMB, Museum für Naturkunde und der Universität Humboldt zu Berlin, Berlin, Germany.

Numbers with Q666C, 0CDN, 0M9H prefixes are the cross-reference sample numbers collected for the United States National Cancer Institute, under the 'Collection of Shallow-water Organisms' program, by the Australian Institute of Marine Sciences, CRRF and MAGNT (subcontracted through CRRF) respectively.

#### TAXONOMY

##### Family Dictyonellidae Van Soest, Diaz & Pomponi, 1990

##### Genus *Acanthella* Schmidt, 1862

Gender feminine. Type species, by monotypy, *Acanthella acuta* Schmidt, 1862. Recent, Adriatic Sea.

##### *Acanthella cavernosa* Dendy, 1922

(Figs 1, 2A,B; Table 1)

*Acanthella cavernosa* Dendy, 1922: 120; Van Soest 1989; Hooper *et al.* 1992 [in part]; Alvarez *et al.* 2000: 195. Not Burton 1934: 565 and Hooper & Lévi 1993: 1414, fig. 13B–D [= *Acanthella klethra* Pulitzer-Finali, 1982: 93]. Not Alvarez *et al.* 2007 [= *Acanthella pulcherrima* Ridley & Dendy, 1886].

*Acanthella pulcherrima*.—Capon & Macleod 1988.

*Acanthella* ? *stipitata*.—Ridley & Dendy 1887: 178.

**Material examined.** TYPE MATERIAL.—*Acanthella cavernosa*: HOLOTYPE, BMNH 1921.11.7.100, Amirante,

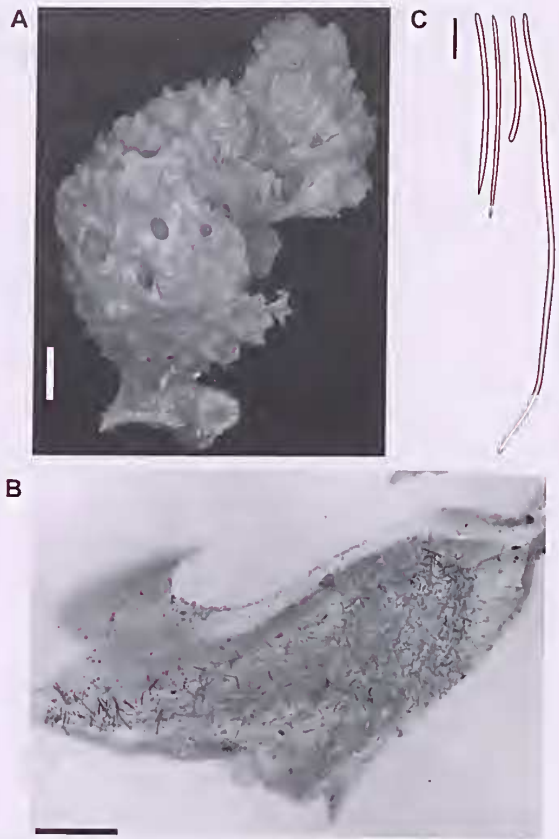


Fig. 1. *Acanthella cavernosa*: A, Holotype, BMNH 1921.11.7.100. B, light micrograph of skeleton (BMNH 1921.11.7.100). Scale bars: A, 2 cm; B, 500 µm, C, 100 µm.

60 m depth, 17 October 1905, coll. HMS Sealark (Fig. 1A). ADDITIONAL SPECIMENS.—Burton's record, BMNH 1930.8.13.142, off North Anchorage, 18 m depth, 17 October 1928, coll. Great Barrier Expedition, Agassiz trawl. Ridley & Dendy's record, BMNH 1887.5.2.73, off Cape York, Torres Strait, 8 September 1874, coll. HMS Challenger. *Acanthella klethra* Pulitzer-Finali, 1982: Holotype MSNG CE 46927, Wistari Reef (Capricorn Group), 7 m depth, 24 April 1979; paratype MSNG CE 46928, Heron Island, reef slope, "Blue Pools" area, 15 m depth, 23 August 1980; paratype MSNG CE 46929, Heron Island, north reef slope, "Blue Pools" area, 15 m depth, 3 October 1979. *Acanthella xutha* (De Laubenfels, 1954), holotype, USNM 23097, Caroline Islands, Truck Islands, Kuop atoll, 2 m depth, 17 August 1949, coll. M.W. De Laubenfels. Indian Ocean: ZMA Por. 10989, -5.6833, 53.5833, Seychelles, Ile Desroches, Atoll, W. rim, 10 m depth, 30 December 1992, coll. R.W.M. van Soest. Papua New Guinea: G312925, Z.3572. Darwin Harbour: G303338, Z.2092, Z.2633, Z.5168 (0M9H2086-K), Z.5856, Z.5871. Wessel Is; Z.5172 (0M9H2702-F). Malaysia: Z.5861-Z.5862, Z.5866-Z.5868. Gulf of Carpentaria, G303512.

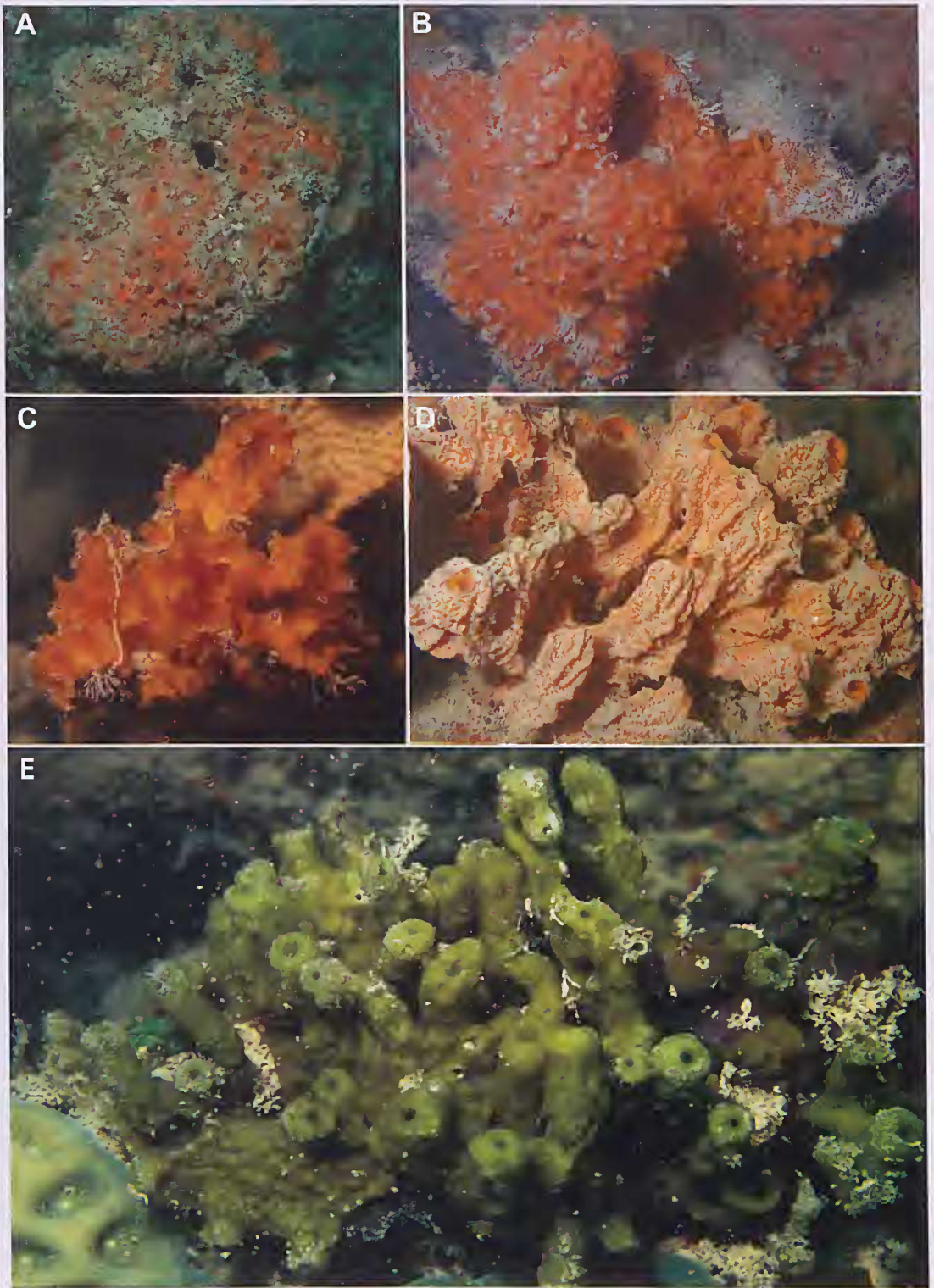


Fig. 2. *Acanthella cavernosa*: A, specimen at Rimbija I., Wessel Is; B, specimen *in situ* in Darwin Harbour. *Acanthella pulcherrima*: C, Z.5870 *in situ* in Darwin Harbour; D, specimen *in situ* in Raragala I., Wessel Is. *Dictyonella chlorophyllacea* sp. nov.: E, specimen *in situ* in Darwin Harbour. Photographs: A,B,E – M. Browne; C – B. Alvarez; D – P. Colin.

**Description.** Shape. (Figs 1A, 2A,B) Variable with 3 basic morphotypes: massive to semi-spherical; bushy with flat-spikey branches arising from multiple bases or from short peduncle, with crowded and complex branching, or in honeycombed reticulation; lobate-tubular with thick lobes joined at base. Transitional forms between these morphotypes in any combination are common.

**Colour.** Generally orange, but beige specimens also found (e.g. G303512); beige in alcohol

**Oscula.** Terminal at lobes or branches, with membranous rims slightly elevated, less than 10 mm in diameter; or flushed and irregularly distributed. Minute ostia aggregated in surface grooves.

**Surface.** Clathrate, rubbery, cartilaginous membranous skin with blunt or spikey short conules, irregularly or evenly distributed, fused laterally forming ridges; sometimes with shallow grooves of irregular shape.

**Skeleton** (Fig. 1B). Cavemous, with dendritic and ascending axes of interwoven spicules echinated by single spicules or short tracts.

**Spicules** (Fig. 1C, Table 1). Strongyles thick and thin (mostly broken), 430–1824 (or longer)  $\times$  2–15  $\mu$ m. Styles straight, slightly bent or curved, 262–1402  $\times$  3–21  $\mu$ m. Styles in same size category with rounded ends, slightly sinuous, or bent near base, less frequent. Anisoxeas transitional to styles, less frequent, 310–798.44  $\times$  5–15  $\mu$ m.

**Remarks.** The holotype of *Acanthella cavernosa* was re-examined (Fig. 1A). The specimen is globular to elongated, 8 cm high by 5 cm maximum width, attached to a narrow and short base, soft and compressible. Its surface is marked by thick choanosomal fibres projecting in short and blunt conules, up to 2 mm long, organised in longitudinal rows in some areas. An organic, slightly transparent membrane stretches over the conules and

fibres. The oscules are irregularly distributed, conspicuous, up to 5 mm in diameter, flush and opening at the surface membrane. The external morphological features of the species are however much more variable as shown in the material examined. Several morphotypes can be identified among the specimens we have studied, but as in other species of Halichondrida, particularly those of Axinellidae (e.g. *Axinella arnensis*; Alvarez & Hooper 2009), they cannot be easily separated, but placed into a gradient of variation with intermediate forms that share a combination of characteristics. Skeletal features and spicule composition and dimensions in *Acanthella cavernosa* seem to be more homogeneous among the material we studied and these allow its differentiation from other very similar species such as *Acanthella pulcherrima* (see below).

The specimen from the GBR recorded by Burton (1934) was also re-examined and compared to additional material from the GBR and Palau. All of these specimens are similar in external morphology to *Acanthella cavernosa* but they differ from this species in skeletal architecture. They are characterised by the presence of fragile (always broken in microscopic slide preparations) and thin strongyles interwoven in the main skeletal axes (appearing as hair-lines in the sections) and lightly bounded by ill-defined spongin fibres, and styles with oxocote modifications. We conclude that these specimens are conspecific with *Acanthella klethra* Pulitzer-Finali, 1982 from the GBR, a species included as a synonym of *Acanthella cavernosa* Dendy, 1922 by Hooper & Wiedenmayer (1994), but considered here as valid. *Acanthella klethra* is also very similar to a central Pacific species, *Axinella xutha* De Laubenfels, 1954, but examination of the type material indicates that the species is better allocated to *Acanthella*, and is likely to be conspecific with Pulitzer-Finali's species (which would make De

**Table 1.** Comparison of spicule dimensions among specimens of *Acanthella cavernosa*. Measurements in micrometres.

Specimen	Locality	Strongyles	Styles	Anisoxeas
BMNH 1921.11.7.100	Amirante, Indian Ocean	779.6–1824.8 (1046.7 $\pm$ 194) $\times$ 4.7–11.4 (7.5 $\pm$ 1.7)	306–509.8 (416.3 $\pm$ 60) $\times$ 7–21.4 (15.3 $\pm$ 4.5)	
BMNH 1887.5.2.73	Torres Strait	undetermined broken $\times$ 2.9–6.7 (4.8 $\pm$ 1)	270.7–745.1 (431 $\pm$ 108) $\times$ 4.8–13.6 (8.8 $\pm$ 1.7)	
ZMA Por. 10989	Seychelles Is	520–1400 (901 $\pm$ 285.6) [10] $\times$ 8–15 (11.2 $\pm$ 2.1) [10]	303–740 (427.2 $\pm$ 87.9)	310–670 (436.3 $\pm$ 85.5) [16] $\times$ 5–15 (9.1 $\pm$ 2.1) [16]
G312925	Papua New Guinea	466.04–1430.35 (977.12 $\pm$ 222.58) $\times$ 3.05–11.11 (8.04 $\pm$ 1.99)	312.11–1402.77 (510.56 $\pm$ 279.19) $\times$ 3.78–12.68 (7.85 $\pm$ 2.15)	355.43–798.44 (500.47 $\pm$ 202.72) [4] $\times$ 6.8–9.93 (8.28 $\pm$ 1.29) [4]
Z.5861	Malaysia	571.94–996.2 (780.42 $\pm$ 105.42) $\times$ 4.74–11.14 (6.94 $\pm$ 1.64)	277.57–645.4 (446.96 $\pm$ 86.35) $\times$ 5.97–12.06 (9.05 $\pm$ 1.43)	
Z.5856	Darwin Harbour	636.7–1200.21 (851.4 $\pm$ 139.91) $\times$ 2.34–8.92 (4.8 $\pm$ 1.76)	262.54–682.41 (446.48 $\pm$ 107.51) $\times$ 5.39–12.79 (8.31 $\pm$ 1.94)	
Z.5172	Wessel I	s430.03–1115.64 (804.07 $\pm$ 164.79) $\times$ 3.7–14.05 (8.22 $\pm$ 2.12)	279.86–1031.29 (465.99 $\pm$ 147.72) $\times$ 3.05–13.19 (8.67 $\pm$ 2.72)	

Laubenfels' name the senior synonym). At this stage we prefer to keep the species separate, until more material from the central West Pacific can be examined and compared to the type material.

The identity of the specimen identified as *Acanthella* ?*stipitata* by Ridley & Dendy (1887) [not *A. stipitata* Carter, 1881] remains enigmatic. Both the external form and the skeleton resemble also *Acanthella klethra*. The strongyles in this specimen are thin and mostly broken, thus their average length is unable to be determined. The skeleton is slightly halichondroid with poor definition of the ascending axes of the strongyles. Ridley & Dendy were uncertain in the generic allocation of this specimen and compared it with *Acanthella stipitata* (Carter) pointing out the similarities in the spicule composition, but they also commented on the similarity in external form with *Clathria* (*Thalysias*) *vulpina* and indicated affinities with the genus *Echinoclathria*.

**Distribution.** The species is widely distributed, with validated records in several marine provinces: Western Indian Ocean (Seychelles), Sahul Shelf (Bonaparte Coast, Arnhem Coast to Gulf of Carpentaria), Western Coral Triangle (North Borneo and Indonesian ecoregions),

Eastern Coral Triangle (Southeast Papua New Guinea) and Northeastern Australian shelf (Coral Sea).

It is common in shallow waters between 5–20 m depth, but recorded also from deeper waters (down to 60 m, from where the holotype was collected).

***Acanthella pulcherrima* Ridley & Dendy, 1886**

(Figs 2C,D, 3; Table 2)

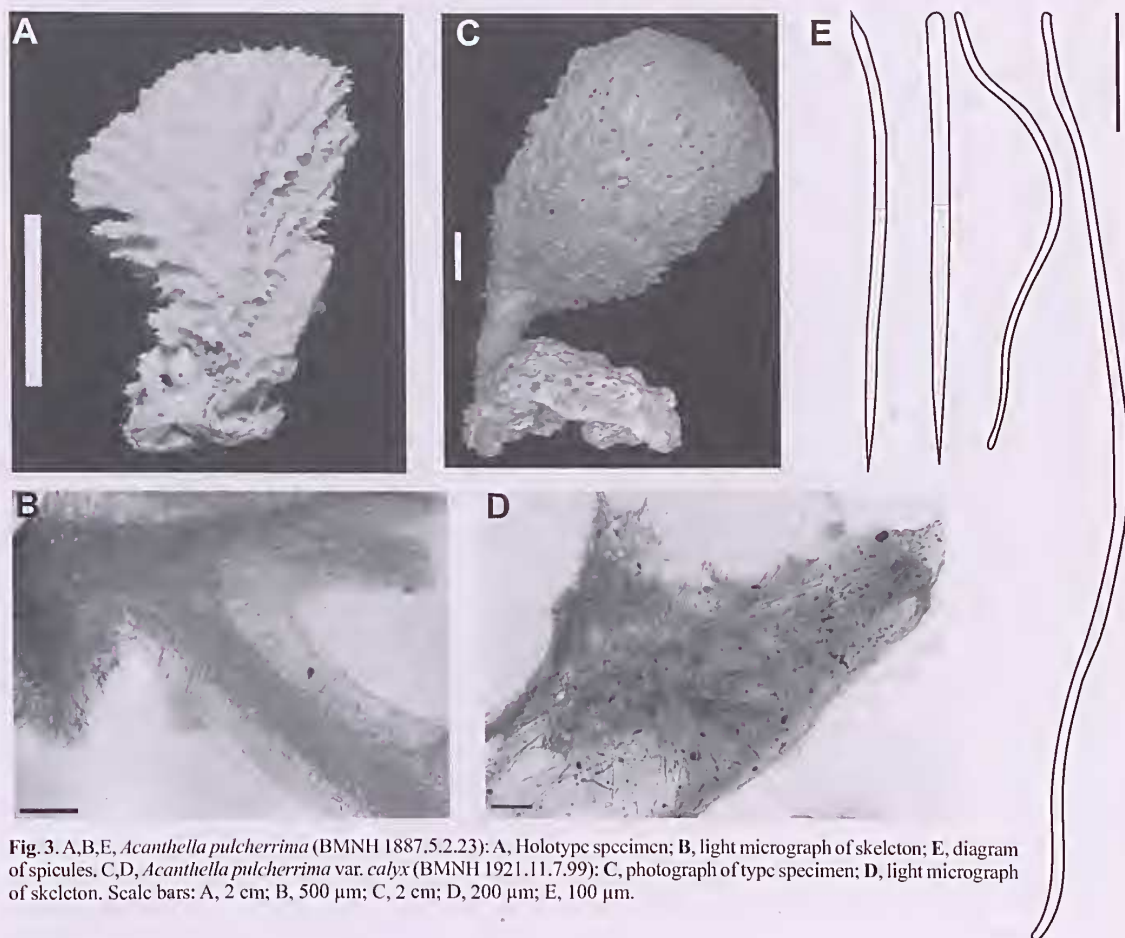
*Acanthella pulcherrima* Ridley & Dendy, 1886: 479; Ridley & Dendy 1887: 177; Alvarez *et al.* 2000: 195. Not Lévi 1998: 103. Not Capon & Macleod 1988 [= *Acanthella cavernosa* Hooper & Wiedenmayer, 1994]. Not *Acanthella pulcherrima* var. *calyx* Dendy, 1922: 120.

*Acanthella* sp. – Ridley 1884: 463.

*Phakellia pulcherrima* – Hooper & Lévi 1993: 1415 [in part]; Hooper & Wiedenmayer 1994: 78.

*Acanthella cavernosa* – Hooper *et al.* 1992 [in part]; Alvarez *et al.* 2007.

**Material examined.** TYPE MATERIAL – *Acanthella pulcherrima*: HOLOTYPE – BMNH 1887.5.2.23, Prince of Wales Chanel, Torres Strait, northern Queensland, 14.5 m depth, 8 September 1874, coll. HMS Alert (Fig. 3A);



**Fig. 3.** A,B,E, *Acanthella pulcherrima* (BMNH 1887.5.2.23): A, Holotype specimen; B, light micrograph of skeleton; E, diagram of spicules. C,D, *Acanthella pulcherrima* var. *calyx* (BMNH 1921.11.7.99): C, photograph of type specimen; D, light micrograph of skeleton. Scale bars: A, 2 cm; B, 500 µm; C, 2 cm; D, 200 µm; E, 100 µm.

*Acanthella pulcherrima* var. *calyx*, BMNH 1921.11.07.099 (Fig. 3C), Cargados Carajos, Indian Ocean, 55 m depth, 28 March 1905, coll. Sealark expedition. OTHER MATERIAL – Hooper & Lévi's (1993) record: G300019, Stn. 102, mid-channel, Canal Woodin, SW. lagoon, 22:23:01° S, 166:48:01° E, New Caledonia, 33 m depth, 28 April 1976, coll. P. Laboute, ORSTOM Noumea. Ashmore Reef, Hibernia Reef and Cartier Reef, WA: G301053, G301091, G301155, Z.2751; Bynoe Harbour: Z.4461 (0M9H2365-N), Z.4487, Z.4489; Z.5169 (0M9H2397-W). Darwin Harbour: G300174, G303386, G303391, Z.429, Z.961 (brown in alcohol), Z.1968, Z.2021, Z.2155, Z.2192, Z.2251, Z.2379, Z.2706, Z.2720, Z.5857, Z.5858, Z.5865, Z.5870; Cobourg Peninsula: Z.2533; English Company Is: Z.3954, Z.3960; Wessel Is: Z.3924, Z.5170 (0M9H2649-V), Z.5171 (0M9H2679-F); eastern Arnhem Land: Z.4493; Gulf of Carpentaria: G303489.

**Description.** Shape (Fig. 2C,D). Erect, semi-spherical or nearly globular, stalked on short or long peduncle, with foliose, bushy, lamellate, pointed or flat branches; complex and crowded branching sometimes in honeycombed reticulation, or forming lobes. Specimens 120 cm in diameter and up to 150 cm high.

Colour. Beige, pale yellow, or orange.

Oscula. Large and apical in lobate specimens, or on margins of branches, variable in size, up to 7 mm diameter, flush with membranous rims slightly elevated.

Surface. Pointed conules irregularly distributed on margins of branches or lobes; cartilaginous, with membranous skin stretching over conules and branches; marked and pierced unevenly by choanosomal spicules and tracts.

Skeleton (Fig. 3B, D). Cavemous, with thick (5–7 mm), ascending columns of interwoven megascleres, dividing irregularly or dendritically, echinated by either plumose tracts, tightly close, diverging towards surface and ending in conules or, by single spicules that occasionally project through surface. Sheets of light spongin, free of spicules, joining main ascending axes in some areas of choanosome.

Spicules (Fig. 3E, Table 2). Sinuous strongyles highly variable in size and thickness, 299–1901 × 2.2–17.9 µm; smaller and thicker strongyles less frequent. Styles straight or slightly bent, few with rounded ends, 252.5–768 × 4.7–19.3 µm. Anisoxeas, with hastate, stepped, blunt or pointed tips, often bent at one end; sometimes slightly crooked or sinuous. Relative proportions between anisoxeas and styles is variable among individuals, but in general anisoxeas dominant.

**Remarks.** *Acanthella pulcherrima* was described by Ridley & Dendy (1886), based on a single specimen from Torres Strait collected during the 'Alert' expedition (Ridley 1884). The type specimen is a small fan, 35 mm high by 29 mm wide, on a peduncle, with its surface marked with longitudinal ridges, up to 3 mm high, that are regularly distributed across the fan. The examination of the northern Australian collections indicates that the external

morphology of this species is much more variable and complex than that exhibited by the holotype (see above). The skeleton and spicule composition of the material we examined corresponds closely to the holotype. Most specimens we examined, including the holotype, have anisoxeas, styles and sinuous strongyles, the latter located in the axis of the thick ascending columns that form the skeleton. The proportion of anisoxeas in relation to styles, is variable among individuals, as seen in species of the genus *Axinella* (Alvarez & Hooper 2009), but anisoxeas in general predominate and styles are less frequent or even absent, as seen in the specimens from Ashmore Reef and Cartier Island, NW Australia. *Acanthella pulcherrima* can easily be confused with *A. cavernosa*, as reflected by the numerous misidentifications reported here. Indeed the two species do share many characteristics. They are similar in shape, but *A. pulcherrima* is generally a stipitate, fan-shaped sponge with a tendency to become bushy and compact. The opposite is seen in *A. cavernosa* which is typically globular-massive shaped and some specimens develop into more erect fan-like forms. The skeletal architecture of both species is nearly identical, but in general the skeleton seems to be more regular in *A. pulcherrima* compared to a less organised skeleton in *A. cavernosa*, and the axes that form the skeleton are slightly thinner. The spicule composition is also similar between the two species, but in general the dominance of anisoxeas relative to styles allows the distinction of *A. pulcherrima* from *A. cavernosa*; the spicule dimensions are quite comparable, and the average length of strongyles is generally longer in *A. cavernosa*.

*Acanthella pulcherrima* was recorded from New Caledonia by Hooper & Lévi (1993) [as *Phakellia*] and by Lévi (1998). Both the external morphology and skeleton of the specimens from New Caledonia are very similar to the holotype; however, and as noted by those authors, it lacks the characteristic anisoxeas present in the holotype from Torres Strait and in the specimens examined here. The populations from New Caledonia were found to be conspecific with material recorded from Taiwan (De Voogd & Alvarez, unpublished data), and probably belong into a new species of *Acanthella* which will be described elsewhere.

The material described by Dendy (1922) from the Indian Ocean (Carjados) as *Acanthella pulcherrima* var. *calyx* [BMNH 1921.11.7.99, examined here Fig. 3C] does not agree with the northern Australian populations of this species either and is considered to be a different species. This specimen has a fleshy consistency, and it is folded into a perfect cup, approximately 7 cm high and 6 cm in diameter, on a narrow and long peduncle. The surface on both sides of the cup is fleshy with conules about 2 mm long, organised in nearly parallel and longitudinal rows. The skeleton is lax, halichondroid, bounded by a moderate amount of slightly darker collagen, occupying the whole thickness of the cup, without clear axes of wavy strongyles, echinated by styles and anisoxeas, as in the holotype of *A. pulcherrima* from Torres Strait. Styles (363.8–632.3 µm

**Table 2.** Comparison of spicule dimensions among specimens of *Acanthella pulcherrima*. Measurements in micrometres.

Specimen	Locality	Strongyles	Styles	Anisoxeas
BMNH1887.52.23 (Holotype)	Torres Strait	476.2–1901.4 (936.6±286.1) x 3.1–17.9 (7.2±3.2)	256.4–420 (331.2±46.1) x 6.7–11.6 (8.7±1.3)	269.1–344.2 (309.3±23) x 4.4–12.1 (8.3±1.9)
Z.2751	Ashmore Reef	213.6–944.7 (591.7±253.8) x 1.5–8.6 (4.6±2.5)	355.6–904.4 (601.7±173.8) [21] x 4.7–12.2 (7.4±1.8) [21]	247.3–420 (313±38.8) x 4.1–10.4 (6.9±2.1)
Z.4461	Bynoe Harbour	298.9–597.6 (434.8±82.5) x 2.2–7.1 (4±1.3)	288.6–701 (413±108.6) x 5.2–14.6 (10.3±2.3)	298.1–426.4 (363.7±40.5) x 8.9–14.1 (10.8±1.5)
Z.5870	Darwin Harbour	388.5–1199.8 (794.2±188.4) x 4–17.3 (9.2±2.7)	252.5–706.9 (484.7±94.5) x 9.7–19.3 (13.6±2.7)	337.9–488.4 (412.9±46.3) x 8.2–15.6 (11.6±2)
Z.2533	Cobourg Peninsula	580–1055.4 (781±199.4) [4] x 4.4–9.9 (7.9±2.5) [4]	288.4–716.5 (404.5±102.4) [20] x 7.6–16.8 (11.5±2.2) [20]	268.8–493.7 (368.1±52.9) x 7.3–15.7 (11.8±2.3)
Z.3954	English Company Is	592.2–1028.2 (895.5±144) [8] x 3.7–7 (5.4±1.2) [8]	374.1–768 (499.5±116.9) [19] x 4.7–11.2 (7.5±1.6) [19]	258.5–604.3 (364.5±94.2) x 5.4–10 (7.1±1.1)
Z.3924	Wessel Is	616.3–954.3 (763.3±96.3) [10] x 4.3–8.2 (6.2±1.3) [10]	374.3–723.2 (519.6±75.1) x 7–14.4 (10.6±1.8)	243.8–485.9 (346.4±56.9) x 4–11.3 (7.8±1.7)

(518.2±62) x 5–19.4 µm (11.2±3.2) are dominant through the skeleton and project slightly towards the surface or in sparse disorganised groups (Fig. 3D). Less frequent strongyles are found intermixed in the skeleton. Only a few strongyles up to 131.6 µm long by 5.2–8.4 µm thick were found in the slide prepared from the holotype and a few anisoxeas, measuring 448.6–492.8 µm x 10.5–10.6 µm, were also present. The specimen could be mistaken for a species of *Stylissa*, but strongyles are not included in the diagnoses of that genus (see below).

**Distribution.** The species is common in northern Australia with validated records from the Northwest Australian Shelf and the Sahul Shelf where it is found in shallow waters from 10–50 m depth and associated with muddy and sandy bottoms. Its distribution might also extend to the Northeast Australian shelf (Coral Sea) according to unverified records at the QM. It is also known from other localities in Indonesia (Alvarez & De Voogd, unpublished data).

**Discussion on the genus *Acanthella*.** The genus *Acanthella* includes 32 valid species according to the *World Porifera Database* (Van Soest *et al.* 2008). Only two of these (*A. cavernosa* and *A. pulcherrima*) are represented in northern Australia. Other species of *Acanthella* reported from Australia (Hooper & Wiedenmayer 1994) are: *Acanthella? costata* Kieschniek, 1900, a dubious species first recorded from Indonesia; *Acanthella inflexa* Pulitzer-Finali, 1982, which does not agree with the concept of the genus and is better allocated to *Stylissa* (see below); *A. klethra* Pulitzer-Finali, 1982, from the GBR, a species very similar to *A. cavernosa*, but considered here as valid after re-examination of the holotype and recent material from the GBR and Palau; and *A. tenuispiculata* Dendy, 1897 recorded from Port Phillip Heads, Victoria. Other Australian species currently accepted under *Phakellia*, mainly from southern Australia, such as *P. carduus* (Lamarek, 1814), *P. dendyi* Bergquist, 1970 and *P. stipitata* Carter, 1881, also

belong to *Acanthella*. None of the later species were found in the study area.

The plasticity of the external morphology and the similarity of skeletal architecture and composition and dimensions of the spicules in species of *Acanthella* have confused authors for decades and as a consequence species have been misidentified regularly as *Axinella* and *Phakellia*. Species of *Acanthella* fall in a gradient of variation with fuzzy limits as in other axinellid genera. The distribution of the species generally overlaps, as in the case of the northern Australian species, making the separation of species even more difficult. It is also possible that some species might be a complex of cryptic species or part of an hybridisation series.

Phylogenetic relationships derived from molecular studies (Alvarez *et al.* 2000; Erpenbeck *et al.* 2005b, 2006) show strong support (i.e. with strong bootstrap values) for some species of *Acanthella*, including the type species of the genus *A. acuta* Smith, 1862, to be closely related to species of *Cymbastela*, a characteristic genus of the Axinellidae, with cup-shaped morphology and a regular plumo-reticulated skeleton and with only oxeas. The skeleton of *Cymbastela* differs greatly from *Acanthella*, which is dendritic with the spicules densely packed in thick axes or columns and echinated either with individual spicules or short plumose tracts of spicules. The consistency of the species included in the two genera is also very different. *Acanthella* is characteristically cartilaginous and *Cymbastela* is soft and velvety. The phylogenetic relationships derived from molecular studies remain at this stage intriguing but unexplained.

Molecular genetic studies (e.g. microsatellite analyses or DNA sequences of appropriate genes) of local populations of *Acanthella* taxa are therefore essential for the delimitation of species within the genus and testing of the species hypotheses presented here. In the meantime, allocation to *Acanthella* using traditional morphological characters will remain imprecise.

**Genus *Dictyonella* Schmidt, 1868**

Gender feminine. Type species, by subsequent designation of De Laubenfels (1936), *Dictyonella cactus* Schmidt, 1868. Recent, Adriatic Sea.

***Dictyonella chlorophyllacea* sp. nov**

(Figs 2E, 4; Table 3)

**Material examined.** HOLOTYPE – Z.5018 (0M9H2121), Weed Reef, entrance to West Arm, Darwin Harbour, 12°29.338'S, 130°48.019'E, 4–10 m depth, 2 August 2002, coll. B. Alvarez & party. PARATYPE – Z.5177 (0M9H2564-F), Nightcliff bommies, off Nightcliff jetty, Darwin Harbour, 12°22.751'S, 130°50.116'E, 5–8 m depth, 8 August 2003, coll. B. Alvarez & party. ADDITIONAL (NON-TYPE) SPECIMENS – Bynoc Harbour, Fish Reef, G303449, Darwin Harbour: QM G300220 (NTM Z.3177), NTM Z.3199, Z.5175 (0M9H2262-Z), Z.5176 (0M9H2264-C), Z.5896.

**Description.** Shape (Fig. 2E). Thickly lamellate (up to 20 cm) or thickly encrusting (up to 10 cm thick), with small tubular projections up to 40 mm long and approximately 5–10 mm diameter. Growing in patches approximately 25 cm in maximum diameter, following substrate.

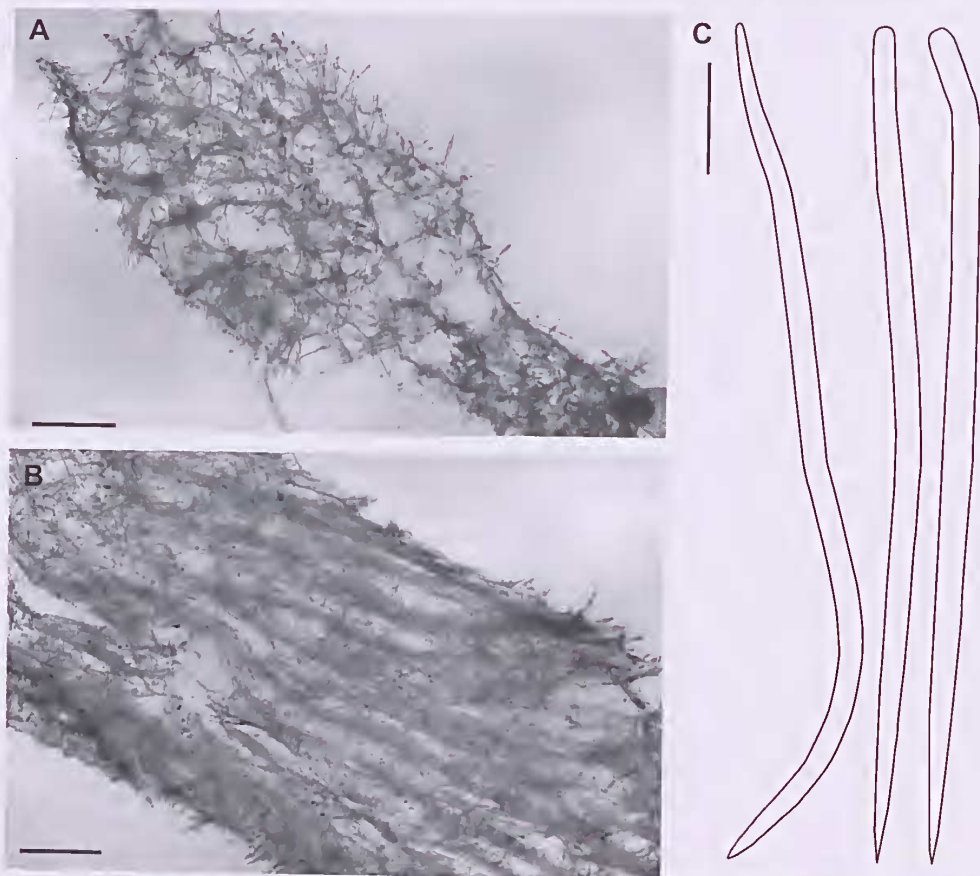
**Colour.** Deep green-purple on shaded side

**Oscula.** Terminal on the small tubular projections.

**Surface.** Nodulose, with small rounded tubercles; hispid, with choanosomal spicules projecting slightly through a membranous ectosome; slightly felty texture; marked by shallow grooves irregularly shaped but sometimes running longitudinally along the tubes or branches.

**Skeleton** (Fig. 4A,B). Halichondroid to plumoreticulated, with longitudinal wavy multispicular tracts, generally ascending and anastomosing towards surface, irregularly connected by single spicules, or short multispicular tracts oriented in any direction. Main skeletal tracts end at surface in brushes of few spicules that project through the membranous ectosome. Skeleton at subectosomal region might become dense and quite halichondroid. Spongin is scarce.

**Spicules** (Fig. 4C, Table 3). Styles, often slightly sinuous or bent at base or with rounded ends, 200–438 × 5–16 µm. Twisted or sinuous oxeas, some transitional to styles, located generally at subectosomal region, less frequent and in same size category of main styles. Thin forms of styles, 2–4 µm thick, are very common in some specimens.



**Fig. 4.** *Dictyonella chlorophyllacea* sp. nov.: A, Holotype, Z.5018, light micrograph of skeleton; B, Paratype, Z.5177, light micrograph of skeleton; C, diagram of spicules. Scale bars: A,B, 500 µm; C, 50 µm.

**Table 3.** Comparison of spicule dimensions among specimens of *Dictyonella chlorophyllacea*. Measurements in micrometres.

Specimen	Locality	Styles
G303449	Bynoe Harbour	335.4–438.5 (374.1±30.2) x 9.2–15.8 (12.3±1.7)
Z.5018	Darwin Harbour	272.2–426.6 (379.6±38.1) x 4.8–14.8 (9.7±2.7)
Z.5177	Darwin Harbour	200.8–412.3 (344±43.7) x 4.8–12.7 (9.2±1.8)

**Distribution.** The species is not common in northern Australia with only isolated populations at Bynoe Harbour and Darwin Harbour. It is found between 3–12 m depth. Also known from East Kalimantan, Indonesia (Alvarez & De Voogd unpublished).

**Etymology.** The species is named after its ability to accumulate chlorophyll.

**Remarks.** *Dictyonella chlorophyllacea* is characteristically covered by a green veneer, with resident cyanobacterial symbionts testing positive for chlorophyll (Hooper unpublished).

The species is assigned to *Dictyonella* with some reservation. Most features agree with that genus, especially the external morphology and surface characteristics; however, the majority of *Dictyonella* species have longer styles than the present one. The closest species to *D. chlorophyllacea* is *D. conglomerata* (Dendy, 1922) from the Indian Ocean, but the skeleton of that species is disorganised compared to the one of *D. chlorophyllacea* which is almost plumoreticulated thus resembling skeletons observed in Axinellidae.

Other species described in *Dictyonella* from the central Indo-Pacific are *D. australiensis* Pulitzer-Finali, 1982 (type material MSNG CE 46934–46935, examined here) which is better allocated to *Scopalina*, and *D. dasiphylla* De Laubenfels, 1954 (holotype USNM 23102, examined here) which is a member of the Raspailiidae and should be synonymised with *Thrinacophora agariciformis* Ridley & Dendy, 1886.

#### Genus *Phakettia* De Laubenfels, 1936

Gender feminine. Type species, by original designation of De Laubenfels (1936), *Phakettia cactoides* Burton, 1928. Recent, Indian Ocean.

##### *Phakettia euctimena* (Hentschel, 1912) new comb.

(Figs 5A,B, 6; Table 4)

*Acanthella euctimena* Hentschel, 1912: 414

**Material examined.** HOLOTYPE – SMF 1012, Aru Is, SW Von Lola, 8–10 m depth, 1 April 1908, coll. H. Merton. ADDITIONAL SPECIMENS – Papua New Guinea: QM G312921, G312938. Ashmore Reef: G300180 (NTM Z.2792), Z.2774, Z.2793. Parry Shoals: Z.3126 (G300580). Darwin Harbour: Z.2047, Z.5173 (0M9H2089-N), Z.5174 (0M9H2279-T). Gulf of Carpentaria: G303495, G311853 (Q66C4687-L, G300758). Wessel Is: Z.3914, Z.5167 (0M9H2660-J)

**Description.** Shape (Fig. 5A,B). Fan-shaped, bushy, or with single or multiple erect digits, branches or tubes, projecting from common broad base with sides partially fused. Projections slightly flattened, bulbous, or pointed. Specimens reach up to 140 mm high and 130 mm diameter.

Colour. Orange or beige

Consistency and texture. Compressible to spongy; rough sandpaper-like texture.

Oscula. Located at ends of branches or projections.

Surface. Membranous ectosome, micro-hispid, shaggy, micro-conulose to conulose, tuberculate, convoluted with fused ridges.

Skeleton (Fig. 6A). Ectosomal skeleton not specialised; covered by dermal skin. Choanosomal skeleton compressed at base; generally halichondroid, formed by multiple multispicular vaguely plumose tracts, fanning out towards surface and with ends of spicules projecting through ectosome; connected irregularly by numerous spicules with disorganised arrangement. High spicule density and low spongin.

Spicules (Fig. 6B, Table 4). Thick styles in wide size range, 322–1402 µm in length; but thin forms also common. Subtylostyles with bases slightly twisted also common, especially in the smaller size categories.

**Remarks.** This species was initially allocated to *Acanthella* by Hentschel (1912). Although aspects of the surface and consistency agree with that genus, the general architecture of the skeleton and the spicule composition correspond to *Phakettia* (see remarks of the genus below).

**Distribution.** The type species was previously known only from the Aru Is, Indonesia (Sahul Shelf province, Arafura Sea), but the present work extends this distribution to include two additional ecoregions of the Sahul Shelf (i.e. Bonaparte Coast and Arnhem Coast to Gulf of Carpentaria), as well as the Northwest Australian shelf (Exmouth to Broome) and the Eastern Coral Triangle (Southeast Papua New Guinea) provinces. The species is found between 4 and 50 m depth.

**Table 4.** Comparison of spicule dimensions among specimens of *Phakettia euctimena*. Measurements in micrometres.

Specimen	Locality	Styles
SMF 1912 (Holotype)	Aru Islands	321.6–1061.3 (602±143.1) x 10.6–28.5 (21.7±4.8)
G312938	Papua New Guinea	483.1–947.7 (748.4±110.9) x 11.3–21.7 (15.9±2.4)
G300180	Ashmore Reef	431.3–790.1 (521.1±70.3) x 10–21.2 (15.9±2.9)
Z.5173	Darwin Harbour	416.9–1402.3 (817.2±292.9) x 8.1–31 (19.6±6.1)
Z.5167	Wessel Is	419.6–1156.5 (730.7±199.4) x 5.8–24.1 (13.9±5.4)

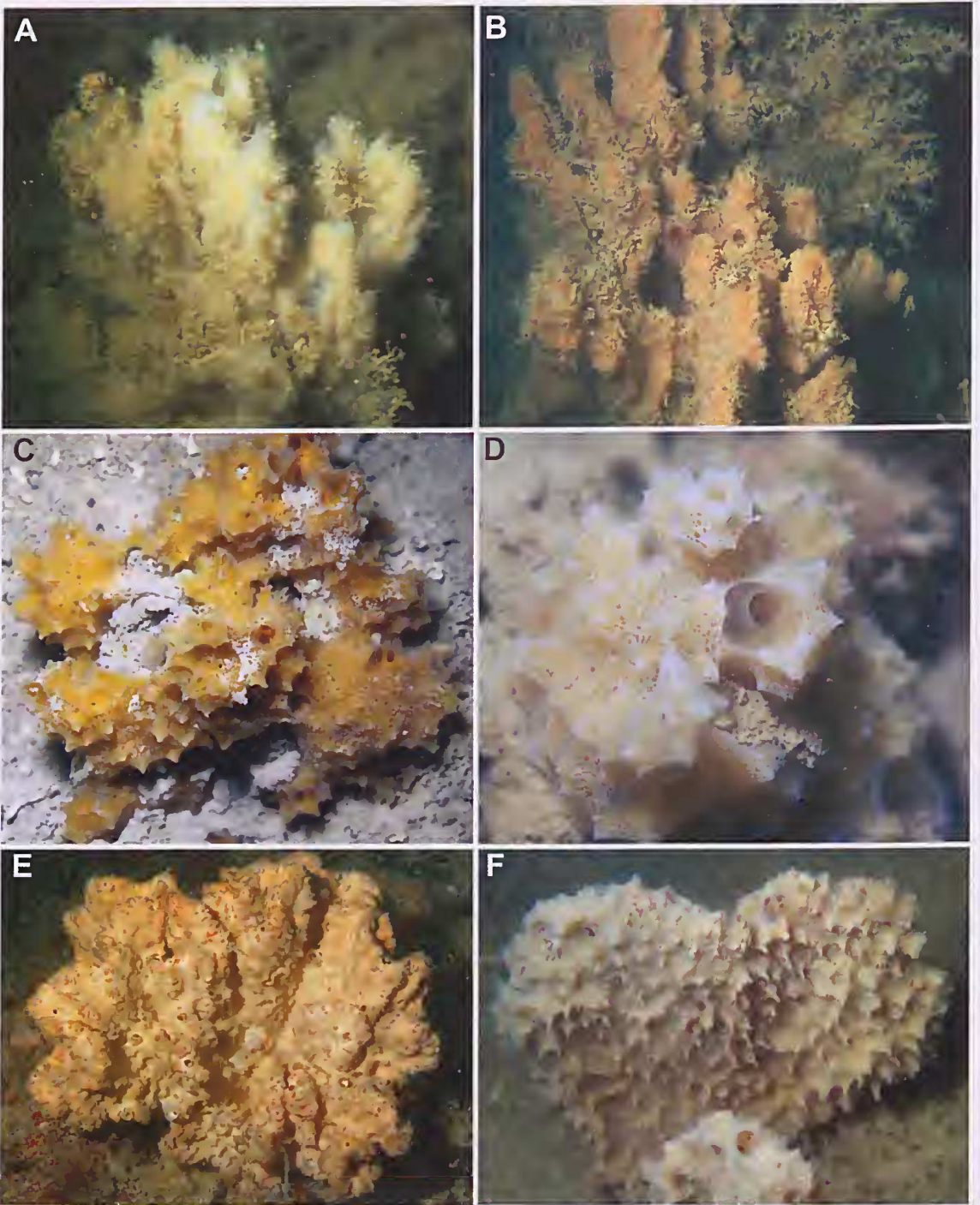


Fig. 5. A,B, *Phakettia euctimena*: specimens *in situ* from Darwin Harbour, cream and orange colour forms. C,D, *Scopalina hapalia*: C, specimen *in situ* from Bynoe Harbour; D, specimen *in situ* from Bynoe Harbour, detail of surface; E, *Stylissa carteri*, specimen *in situ* from Wessel Is; F, *Stylissa flabelliformis*, specimen *in situ* from Darwin Harbour. Photographs: A,B,D – B. Alvarez; C – H. Nguyen; E,F – P. Colin.



Fig. 6. *Phakettia euctimena*; A, Z.5173, light micrograph of skeleton; B, diagram of spicules. Scale bars: A, 500 µm; B, 100 µm.

***Phakettia virgultosa* (Carter, 1887) new comb.**

(Fig. 7; Table 5)

*Axinella virgultosa* Carter, 1887: 68, pl. 5, fig. 11.

**Material examined.** HOLOTYPE – BMNH 1887.4.26.3 (fragment of the type) and 1889.6.9.3, King Is, Mergui Archipelago, coll. J. Anderson. ADDITIONAL SPECIMENS – Darwin Harbour: Z.421, Z.5694. Gulf of Carpentaria: G303494.

**Description.** Shape (Fig. 7A). Generally small specimens, with thin ‘fringe-like shreds’ projecting from broad base.

Colour. Orange or cream-brown.

Consistency and texture. Soft and delicate.

Oscula. Not visible.

Surface. Hispid, with spicules projecting through erect projections. Transparent membrane covering surface at base.

Skeleton (Fig. 7B). Thick dendritic axes, multispicular, running longitudinally along erect filamentous processes; regularly plumo-echinated by spicules, single or in thin brushes (3–5). Skeleton at base halichondroid.

Spicules (Fig. 7C; Table 5). Thick styles, commonly slightly sinuous or crooked, occasionally with rounded ends; some much smaller with enlarged and recurved bases, located at base of specimen, others some with rounded ends. Styles with recurved bases (some nearly rhabdostyles) common (particularly in specimen G303494), generally less than 500 µm long, but cannot be distinguished as a separate size class. A transitional series from recurved bases to straight styles is found in large size range (173.4–1214.5 x 5–24 µm).

**Remarks.** Two fragments of what appears to be the holotype of this species were examined at the BMNH. Its characteristics coincide with both Carter’s (1887) description and figure and with the rest of the material examined and allocated to this species. Carter (1887) assigned the species to *Axinella*, but it agrees with the

current definition of *Phakettia* and therefore is referred here to that genus.

**Distribution.** The species was initially recorded from the Mergui Archipelago (Andaman Sea province), and it is now recorded from northern Australia (Sahul Shelf province, including Bonaparte Coast and Arnhem Coast to the Gulf of Carpentaria). It is found from the intertidal zone to a depth of 52 m.

**Remarks on *Phakettia*.** De Laubenfels (1936) erected *Phakettia* for species generally included in *Phakellia* but with styles as the only type of megasclere. The definition of the genus was revised by Van Soest *et al.* (2002) based on the redescription of the type species (*Phakettia cactoides*) and reserved for species with a central region of long styles in a confused and dense mass from which they radiate outwards. The two species described above fit the expanded definition of *Phakettia* well and are therefore included in this genus.

De Laubenfels (1936) suggested further species should be included in *Phakettia*. Most of these are now accepted either in their original genera or in different combinations (see Van Soest *et al.* 2008). Of the species suggested by De Laubenfels for *Phakettia*, only *Phakellia fusca* Thiele, 1899 and *Phakellia ridleyi* Dendy, 1887 could possibly

Table 5. Comparison of spicule dimensions among specimens of *Phakettia virgultosa*. Measurements in micrometres.

Specimen	Locality	Styles
BMNH 1889.6.9.3 (Holotype)	Indian Ocean	301.8–829.4 (696.6±150.2) x 8.3–22.8 (15±3.6)
Z.421	Darwin Harbour, Lee Point	497.9–1011.4 (800.2±126.6) x 5–21.5 (13.4±4.5)
Z5694	Darwin Harbour, Channel 1.	487–717.3 (636.6±57.1) x 11.3–19 (15.5±1.9)
G303494	Gulf of Carpentaria	173.4–1214.5 (593.3±255.6) x 6.1–24.2 (17.2±4.4)

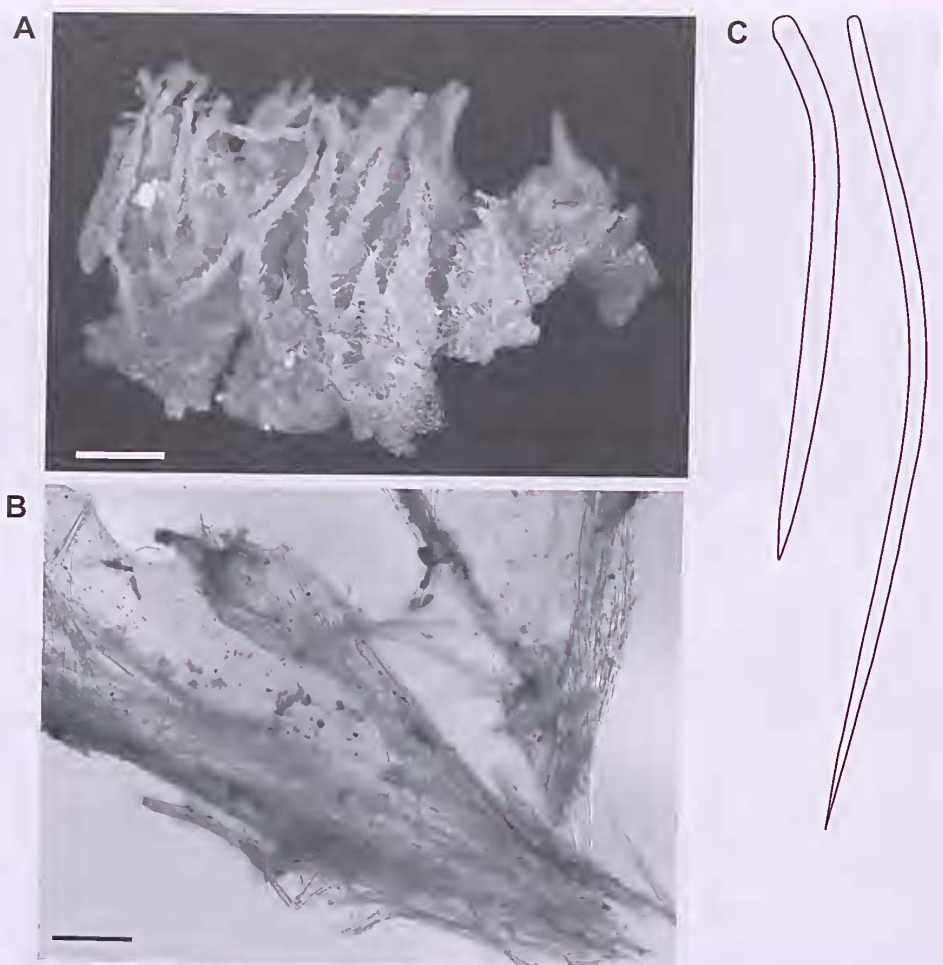


Fig. 7. *Phakettia virgultosa*: A, Holotype, BMNH 1889.6.9.3; B, Z.5694, light micrograph of the skeleton; C, diagram of spicules. Scale bars: A, 2 cm; B, 500 µm; C, 100 µm.

be accepted as members of this genus. We have not been able to re-examine the type specimens of these species so those assignments are subject to confirmation and might support a synonymy between *Phakellia fusca* and *Phakettia euctimena*.

After examination of the type material it is concluded that *Homaxinella domantayi* Lévi, 1961 from the Philippine Is [MNH LBIM DCL698] and *H. phrix* De Laubenfels, 1954 from the Caroline Is [USNM 23080] both belong to *Phakettia*. Both are very similar to *P. euctimena*, but it is necessary to examine more specimens from the populations from the Philippine Is and the Caroline Is to be able to confirm their conspecificity. The skeleton of *P. domantayi* is much denser, highly spiculate and more disorganised. The styles are characteristically robust and less variable in length  $455.1\text{--}855.7\text{ }\mu\text{m}$  ( $645\pm 81.9$ )  $\times$   $14.6\text{--}36.4\text{ }\mu\text{m}$  ( $25.8\pm 5.3$ ) than in *P. euctimena*. *Phakettia phrix* (De Laubenfels, 1954) shares with *P. euctimena* the habit, the characteristic compressible and resilient consistency, and the large range

of sizes of the styles (i.e.  $218.5\text{--}1357.3\text{ }\mu\text{m}$  ( $814.8\pm 405.3$ )  $\times$   $2.3\text{--}13\text{ }\mu\text{m}$  ( $7.8\pm 3.2$ )), but is relatively thinner, more fragile and slightly curved.

#### Genus *Scopalina*

Gender feminine. Type species, by monotypy, *Scopalina lophyropoda* (Schmidt, 1862). Recent, Mediterranean Sea.

#### *Scopalina hapalia* (Hooper, Cook, Hobbs & Kennedy, 1997) comb. nov.

(Figs 5C,D, 8; Table 6)

*Hymeniacidon hapalia* Hooper, Cook, Hobbs & Kennedy, 1997: 58.

**Material examined.** HOLOTYPE – NTM Z.184, Dudley Point Reef, East Point,  $12^{\circ}25.01'\text{S}$ ,  $130^{\circ}48.01'\text{E}$ , intertidal, 13 September 1981, coll. J.N.A. Hooper & party. PARATYPES – QM G303414, N of South Shell I, Darwin Harbour,  $12^{\circ}29.1334'\text{S}$ ,  $130^{\circ}52.16'\text{E}$ , 14 m depth, 25 September 1993, coll. J.N.A. Hooper & L.J. Hobbs. ADDITIONAL SPECIMENS – Papua New Guinea: QM G304789 (0CDN1966V). Bynoe

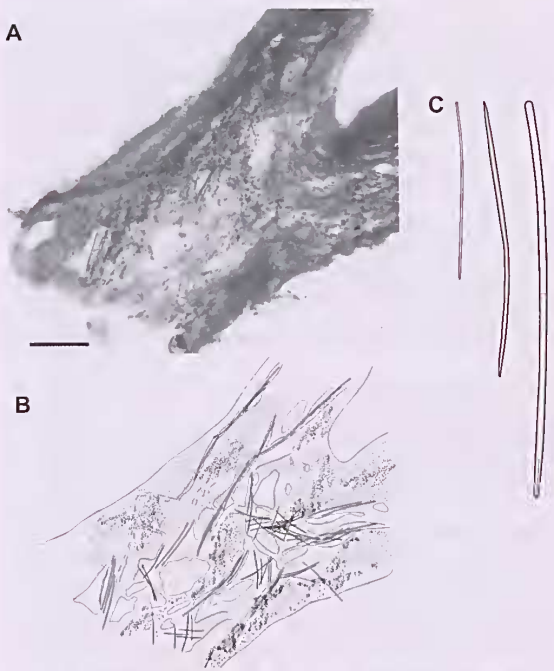


Fig. 8. *Scopalina hapalia*: A, Z.184, light micrograph of skeleton; B, diagram of skeleton; C, diagram of spicules. Scale bars: A, 500  $\mu$ m; C, 100  $\mu$ m.

Harbour: NTM Z.5178 (0M9H2436-P). Darwin Harbour: QM G303280, G315920, NTM Z.272, Z.286, Z.2146, Z.2560, Z.5165 (0M9H2237-X), Z.5882.

**Description.** Shape (Fig. 5C,D). Thickly to thinly encrusting, up to 5–10 mm thick, following contours of substrate and covering areas up to 40 cm in maximum diameter; sometimes with erect and branching projections.

Colour. Orange alive.

Oscula. Flush between conules, with transparent, membranous and elevated rims.

Surface. Transparent ectosome, marked with tangential and neat reticulation of thin spongin [?] fibres (only observable underwater and when specimens are fully expanded) (Fig. 5D), with long spiky conules, or small branching projections.

Consistency and texture. Soft and fleshy, slimy, falling apart and releasing mucus when collected.

Skeleton (Fig. 8A). Basal plate of spongin, very granular, with ill-defined spongin fibres cored by single styles, or paucispicular or multispicular tracts. Skeleton (when examined via light microscope) obscured by granular pigments.

Spicules (Fig. 8B, Table 6). Styles, slightly curved with rough or uneven ends, or stepped, occasionally with rounded ends, 375–662 by 5–17  $\mu$ m. Thinner forms (less than 5  $\mu$ m thick) and in similar length are common, but do not seem to constitute separate class.

**Remarks.** The species was originally described in the genus *Hymeniacidon* with some reservation and under

the assumption that an ectosomal skeleton was absent. It was thought to be related to other poecilosclerids (e.g. *Batzella corticata* or *Strongyladon intermedius*) based on the presence of smaller strongylote styles. However, a re-examination of the type material indicates that the strongylote styles are derived from the thin category of styles and do not constitute a relevant character for the generic allocation of the species.

The species is better allocated to *Scopalina*, a genus not previously reported from Australian waters. *Scopalina hapalia* shares with other species of the genus the soft consistency, the presence of spongin fibres rising up from a basal plate, the ending in conules, and the granular aspect of the choanosome which is probably due to the presence of pigmented granular cells. This is also characteristic of other species of *Scopalina* (Blanquer & Uriz 2008) and other members of Dictyonellidae (i.e. *Svenzea* (Alvarez et al. 2002), *Liosina* and *Stylissa flabelliformis*, see below).

*Scopalina hapalia* is similar to *S. australiensis* Pulitzer-Finali, 1982 (type material MSNG CE 46934 and CE 46935, examined here), but it differs slightly in its spicule composition and the size of the styles. In *S. australiensis* oxeate modifications of styles are common and styles are on average thinner. The choanosome of *S. hapalia* is heavily granular, to the point that is hard to distinguish the structure of the choanosomal skeleton. It needs to be determined whether the amount of granular pigment present in the choanosome of *S. hapalia* is related to the general habitat conditions (silty and turbid) of the northern Australian populations. It is a characteristic found in other species of Dictyonellidae and also across genera (i.e. *Liosina* and *Svenzea*), and therefore might not be of enough significance to separate taxa at the species level.

Populations of *Scopalina* allegedly belonging to one single species (i.e. *Scopalina lophyropoda* Schmit, 1862) from the Mediterranean and the eastern Atlantic were shown to be part of a complex of genetically distinct cryptic species (Blanquer & Uriz 2008) that could be separated only using a combination of morphological characters. It is likely that populations from northern Australia here assigned to *S. hapalia*, might be genetically distinct from those of the northeastern region and currently allocated to *S. australiensis*. Detailed study of these populations might reveal further characteristics of their morphology that could be used for unequivocal separation of species.

**Distribution.** Very common in the area of Darwin Harbour and Bynoe Harbour (Sahul Shelf province, Bonaparte Coast ecoregion), from the intertidal zone to 14 m. It is also found in the Eastern Coral Triangle (Southeast Papua New Guinea).

### Genus *Stylissa*

Gender feminine. Type species, by original designation of Hallmann (1914), *Stylotella flabelliformis* Hentschel, 1912. Recent, Aru Is, Indonesia.

Table 6. Comparison of spicule dimensions among specimens of *Scopalina hapalia*. Measurements in micrometres.

Specimen	Locality	Thick styles	Thin styles
Z.184 (Holotype)	Darwin Harbour	375.1–550.6 (503.4±36.7) x 6.7–11.2 (9±1.2)	320.6–439.6 (376±31.8) x 2.4–4.8 (3.6±0.7)
G303414 (Paratype)	Darwin Harbour	455.6–662.7 (532.7±50.6) x 5.4–16.9 (8.8±2.5)	351.5–619.2 (444±63.3) x 2.7–5.8 (4±0.9)
G304789	Papua New Guinea	419.7–583.4 (521.4±35.4) x 6.3–12 (8.7±1.5)	304.7–463.3 (374.8±49.9) x 2.1–5.8 (3.8±0.9)
Z.5178	Bynoe Harbour	450.7–626.8 (551.5±51.5) x 6.3–15.6 (9.6±2.2)	182–572.5 (427.1±95.1) x 1.5–7.3 (3.4±1.4)

***Stylissa carteri* (Dendy, 1889)**

(Figs 5E, 9; Table 7)

*Acanthella carteri* Dendy, 1889: 93; Dendy 1905: 193; Dendy 1922: 119; Lévi 1961: 16.

*Acanthella aurantiaca* Keller, 1889: 396. – Topsent 1906: 6; row 1911: 356; Van Soest 1989: 228.

*Axinella carteri* – Burton 1959: 258; Thomas 1973: 41; Thomas 1981: 29; Hooper & Lévi 1993: 1410; Hooper & Wiedenmayer 1994: 72; Lévi 1998: 102; Alvarez *et al.* 2000.

*Stylissa carteri* – Van Soest *et al.* 2002: 783.

*Stylissa flabelliformis* – Hooper & Lévi 1993: 1422 [in part]; Erpenbeek *et al.* 2005b: 95.

*Teichaxinella labyrinthica* – Hooper *et al.* 1992: 265.

**Material examined.** LECTOTYPE – BMNH 1889.1.21.53 (here designated), dry, Tuticorin Pearl Banks, Gulf of Manaar, coll. E. Thurston, 1889 (Fig. 9A). Lectotype chosen from three specimens collected by E. Thurston from the Gulf of Manaar, and bearing a hand-written red label: “No. 65, Brit. Mus. Reg. 89.1.21.53. Loc: Gulf of Manaar. Coll. Thurston (2).” PARALECTOTYPES – BMNH 1889.1.21.11, wet, Tuticorin Pearl Banks, Gulf of Manaar, coll. E. Thurston, 1889; BMNH 1890.6.28.4, dry, P. Amban[?], Gulf of Manaar, shallow water, coll. E. Thurston. ADDITIONAL SPECIMENS – *Acanthella aurantiaca* Keller, 1889: ZMB 0182, lectotype

(here designated), dry, Red Sea, coll. Hemprick & Ehrenberg, 1889; ZMB 2921, paralectotype, wet, Suakin, Red Sea, 5 August 1889. Lectotype chosen from two syntypes bearing the original hand-written label: “*Acanthella aurantiaca*, Rothés Meers” and matching Keller’s illustration. Indonesia, Barang Lompo: ZMA Por.17668, 17690. Laeepede Is, Western Australia: NTM Z.2321, Z.2351. Ashmore Reef and Cartier I.: QM G300183, G301051, G301081, G301082, G301094, G301138, G301152, Z.629, Z.2797, Z.2798. Melville I.: Z.37, Z.607, Z.616. Parry Shoals: G310143, Z.3063, Z.3081. Bynoe Harbour: Z.5180 (0M9H2521-I). Darwin Harbour: G303366, Z.2710, Z.5179 (0M9H2291-I). Gunn Point: Z.1447; Cobourg Peninsula: Z.28. Wessel Is: G300750, G311872, Z.3926, Z.5183 (0M9H2604-W).

**Description.** Shape (Fig. 5E). External growth form very variable, with habits including thickly flabellate, digitate, branching, bushy, buttressed, tuft-like, thickly encrusting to bulbous; erect, stipitate, attached to substrate directly or by stalk of variable height and diameter, 20–90 mm long, up to 40 mm diameter; with massive, lobate, irregularly planar or globular projections, up to 350 mm wide or, branches projecting in one or several planes, consisting of relatively thick, flattened planar or buttressed lamellae, 4–11 mm

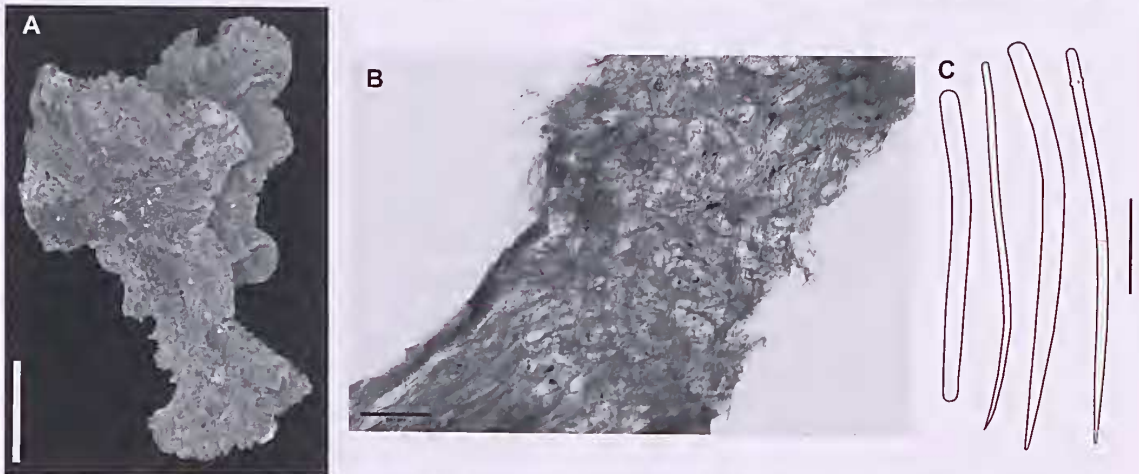


Fig. 9. *Stylissa carteri*: A, Lectotype, BMNH 1889.1.21.53; B, light micrograph of skeleton; C, diagram of spicules. Scale bars: A, 2 cm; B, 500 µm; C, 100 µm.

thick, with irregular margins. Growing from 10–400 mm high.

Colour. Bright, light, pale orange-brown alive (Munsell 2.5YR 7/8), pale orange-brown in ethanol. Surface slightly darker than interior of sponge.

Oscula. Flushed with elevated membranous rims, irregularly distributed.

Surface. Fleshy, conulose, irregularly striated, sculptured, rough; with irregular sharp conules, 3–5 mm high, solitary or joined to form meandering surface ridges. Mottled dusty appearance very characteristic, but not always obvious.

Consistency and texture. Rubbery, compressible, easily torn.

Skeleton (Fig. 9B). Axial skeleton condensed into several multispicular bundles, 100–250 µm wide, running more or less longitudinally through lamellae, fully cored by long slender styles, bound together by very light spongy fibres, and interconnected at irregular angles by vaguely plumose, ascending, paucispicular extra-axial tracts of styles or individual spicules. Fibre reticulation relatively close meshed, with lacunae forming elongate oval chambers, up to 300 x 70 µm. Collagen in mesohyl relatively light compared with ectosomal region.

Spicules (Fig. 9C, Table 7). Single category of style present, though variable in thickness, 272–651 x 4–28 µm, occasionally strongylote; styles relatively long, slender or robust, usually slightly curved symmetrically or towards basal end, sharply pointed, fusiform, with evenly rounded

base or slightly constricted. Relative proportions of thinner and thicker styles also vary within and between populations.

**Remarks.** This species has been moved between *Acanthella* and *Axinella* mainly because it shares a number of characteristics with both genera. The shape and consistency of some individuals are nearly identical to those of species like *Acanthella cavernosa* or *A. pulcherrima* (see above), making it difficult to separate them based on those features alone. *Stylissa carteri* differs from species of *Acanthella* in the organisation of the skeleton and in both spicule composition and dimensions. The strongyles, some of which are sinuous, observed in some specimens led some authors to allocate the species to *Acanthella*. After examination of a large number of specimens it is concluded that those strongyles are derived from styles and they do not constitute a separate type of spicule as in the case of species of *Acanthella* where the strongyles are clearly distinguished from the styles and oxcas, and are mainly located in the core of the choanosomal tracts (or axes).

*Stylissa carteri* closely resembles *S. flabelliformis*, especially individuals from Indonesian populations. The two species share a number of external characteristics, such as shape, surface and colour, but both the skeleton and the spicule composition are distinctive (see below for further discussion).

Conversely, *Stylissa carteri* resembles *S. massa* (Carter, 1887) in skeletal architecture, composition and spicule dimensions, but differs clearly in habit and surface characteristics. The two species can be sympatric (although not in the present study area). Molecular studies indicate that these species are closely related to species of the genus *Axinella* (see below for further discussion on this topic).

**Distribution.** *Stylissa carteri* is a very common species through the Indo-Pacific and its distribution extends well beyond the present study area. Based on reported and verified records the species is present throughout a number of provinces including Red Sea and Gulf of Aden, western Indian Ocean, central Indian Ocean islands, Northwest Australian Shelf, Sahul Shelf, Northeast Australian Shelf, and tropical Southern Pacific Ocean. It is found between 5 and 25 m deep within the study region, but deeper in other provinces (e.g. up to 76 m in the Northwest Australian Shelf province).

Genetic studies of populations might reveal that *Stylissa carteri* constitutes a complex of cryptic species which would explain the wide distribution observed in this species.

Lectotypes for *Acanthella carteri* and its junior synonym *A. aurantiaca* are designated here to provide reference to the species described by Dendy (1889) and Keller (1889) respectively.

#### *Stylissa flabelliformis* (Hentschel, 1912)

(Figs 5F, 10; Table 8)

*Stylotella flabelliformis* Hentschel, 1912:355; Hallmann 1914: 355; Hooper & Lévi 1993[in part]; Van Soest *et al.*

**Table 7.** Comparison of spicule dimensions among specimens of *Stylissa carteri*. Measurements in micrometres.

Specimen	Locality	Styles
1889.01.21.053 (Lectotype)	Indian Ocean, Gulf of Mannar	324.5–453.6 (395.9±33.8) x 6–16.9 (12±3.2)
1889.1.21.11 (Paralectotype)	Indian Ocean, Gulf of Mannar	272.5–510.4 (394.9±58.9) x 11.9–22 (15.9±2.5)
1890.6.28.4 (Paralectotype)	Indian Ocean, Gulf of Mannar	355.7–466.9 (395.4±27) x 4–18.3 (11.2±3)
ZMB0182 (Lectotype of <i>Acanthella</i> <i>aurantiaca</i> )	Red Sea	355.4–651.1 (494.6±56.2) x 10.5–18.6 (14.1±2.3)
ZMB2921 (Paralectotype of <i>Acanthella</i> <i>aurantiaca</i> )	Red Sea	332.7–493.9 (423.9±33.7) x 6.3–14.8 (10.3±2.3)
G301051	Cartier I.	428.5–574.4 (507.8±36.5) x 11.6–28.5 (20.8±4.3)
Z.5180	Bynec Harbour	288.6–442.2 (392.8±37.2) x 7.7–21.5 (15.6±3.3)
Z.5179	Darwin Harbour	325–479.3 (403.1±40.8) x 8–22.5 (16.1±4.2)
Z.5183	Wessel Is	355.9–603.3 (480.3±65.2) x 6.7–17.6 (11.5±3)

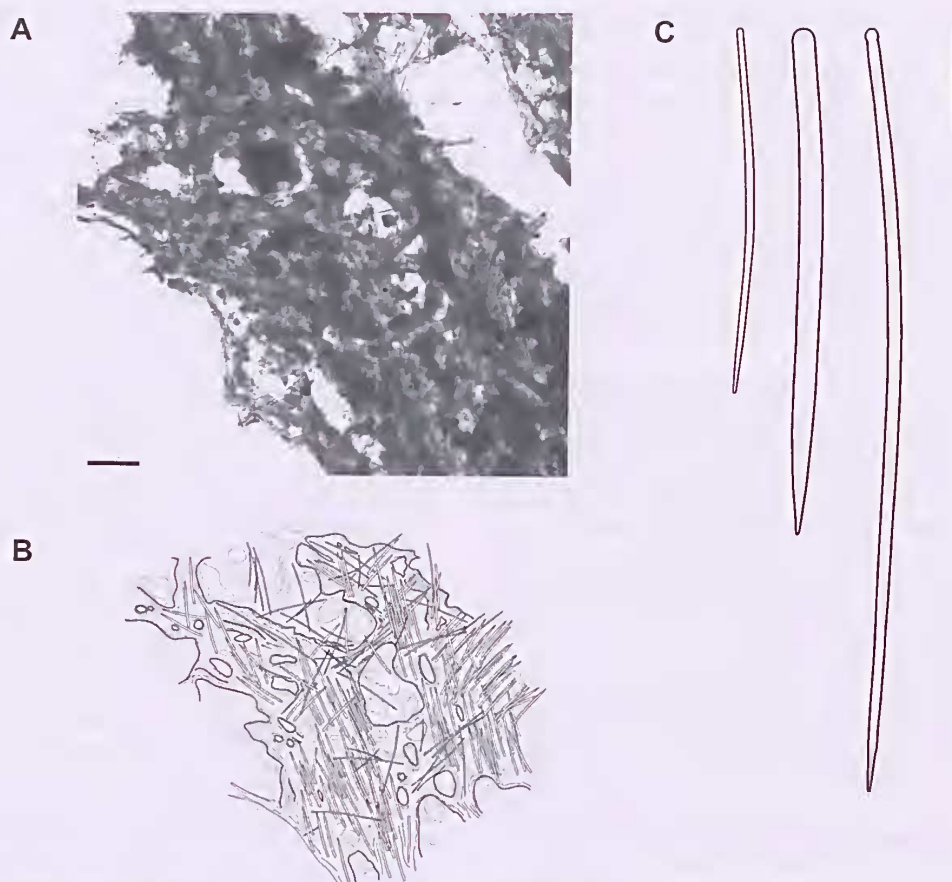


Fig. 10. *Stylissa flabelliformis*: A, SMF 1587, light microphotograph of skeleton; B, diagram of skeleton; C, diagram of spicules. Scale bars: A, 500  $\mu$ m; C, 100  $\mu$ m.

2002: 783. Not Erpenbeek *et al.* 2005b [= *Stylissa carteri* (Dendy, 1889)].

*Ulosa* sp. – Alvarez *et al.* 2000.

**Material examined.** LECTOTYPE designated by Hooper & Lévi (1993) – SMF 1587 Aru Is, SW von Lola, Station 9, Indonesia, 8 m depth, coll. H. Merton, 1 April 1908, dredge. PARALECTOTYPES – Aru Is, Indonesia, coll. H. Merton, dredge, Aru and Kei Is expedition, 1 October 1907, 31 August 1908: SMF 1527, Station 8, 6–10 m depth, 31 March 1908; SMF 1534, Station 8, 8–10 m depth, 1 April 1908; SMF 1538, Station 12, 15 m depth, 8 April 1908; SMF 1689; SMF 1690. ADDITIONAL SPECIMENS – Adele Is, Western Australia: NTM Z.713, Z.718. Bynoe Harbour: Z.5166 (0M9H2435-O), Z.5182 (0M9H2394-T), Z.5886. Darwin Harbour: QM G300143, G303402; NTM Z.87, Z.187, Z.188, Z.189, Z.433, Z.817, Z.862, Z.2654, Z.4456 (0M9H2007-X), Z.5184 (0M9H2101-Z), Z.5885. Cobourg Peninsula: QM G316834. Gulf of Carpentaria: QM G303506, G304937, G304941.

**Description.** Shape (Fig. 5F). Thin fans up to 5 mm thick, uni-planar to multi-planar, on narrow base or

short peduncles; or in form of irregularly shaped digits. Specimens up to 300 mm high.

**Colour.** Pale red, orange, yellow, beige-brown.

**Oscula.** Flush on surface with bubble-like transparent membranes; less than 5 mm in diameter.

**Consistency and texture.** Soft, floppy, fleshy.

**Surface.** Soft, membranous highly conulose, marked with thick choanosomal axes. Soft conules, up to 6 mm long, evenly or irregularly distributed. Dermal membrane transparent, delicate and collapsible out of water, stretched over conules and supported by choanosomal fibres.

**Skeleton** (Fig. 10A). Plumose traets ascending to surface, forming irregular reticulation, enveloped by sheaths or slightly to well-developed spongin fibres. In larger specimens, dendritic choanosomal axes up to 5 mm diameter, oriented longitudinally through fan and becoming thinner close to fan margin, irregularly interconnected, or anastomosing forming, an ill-defined reticulation. Most specimens with characteristic grainy pigment (when observed via light microscope) obscuring arrangement of skeleton.

**Table 8.** Comparison of spicule dimensions among specimens of *Stylissa flabelliformis*. Measurements in micrometres.

Specimen	Locality	Styles	Anisoxeas-oxeas
SMF 1587	Aru Is	401.3–550 (470±47.1) x 6.7–25 (16.6±4.5)	290–540 (436.7±130.5) [3] x 8–25 (15.3±8.7) [3]
SMF 1689	Aru Is	354.5–480.7 (413.7±38.5) x 3.7–14.8 (8.7±3.1)	255.7–442.5 (330.5±60.3) [20] x 6.7–15.7 (9.5±2.1) [20]
SMF 1690	Aru Is	345.4–643.3 (463.8±74.1) x 8.4–22.5 (13.8±2.8)	
Z.718	Adele I., WA	397–530.4 (467.5±41.9) x 4.5–20 (12.6±3.2)	390.7–568.7 (511.2±63.3) [7] x 11.7–22 (17.8±3.5) [7]
Z.5182	Bynoe Harbour	411.6–562.3 (479±44) x 11.1–29 (18.1±4)	387.1–548.9 (495.2±44.8) [15] x 15.7–27.6 (20.9±3) [15]
Z.4456	Darwin Harbour	341.6–518 (437.6±48.6) x 10.8–25.7 (18.7±3.1)	457.2–596.2 (511.4±59.5) [4] x 16.3–19.3 (17.6±1.3) [4]

Spicules (Table 8, Fig. 10B). Styles of variable thickness, some with rounded ends, 341–643 x 3–29 µm. Anisoxeas and oxeas less frequent, with tips stepped or rounded, slightly bent at one-third of total length, 255–596 x 6–27 µm thick; thin forms are common in some specimens.

**Remarks.** As mentioned above, this species is similar to *Stylissa carteri*. Both share a number of characteristics including those of shape, surface and colour. In the field they can be distinguished by consistency, texture and surface characteristics – firm, rubbery and compressible with a discontinuous dust-like dermal membrane in *S. carteri* versus a soft, thin and floppy with a thin transparent membrane in *S. flabelliformis*. The two species can be further distinguished by their skeletal arrangement – robust with thick multispicular bundles forming a close mesh reticulation in *S. carteri* versus a grainy choanosome with thick dendritic fibres/tracts ascending irregularly to the surface and forming an ill-defined reticulation in *S. flabelliformis*.

The surface characteristics of *Stylissa flabelliformis* are remarkably similar to those of species of *Scopalina*, both having long and soft conules and a transparent and collapsible dermal membrane. They also share the grainy appearance of the skeleton (a feature also observed in species of the dictyonellid genus *Svenzea*) and some aspects of the skeletal organisation such as the dendritic fibres ascending to the surface. Furthermore, *Stylissa flabelliformis* was shown to be more closely related to species of *Scopalina* than to *Stylissa carteri* in an analysis based on sequence data from the 28S rDNA (see Alvarez *et al.* 2000). Species of *Scopalina*, however, are encrusting to thickly-encrusting, a feature not observed in *Stylissa flabelliformis*. The close relationship between *Stylissa flabelliformis* (which is the type species of the genus) and species of *Scopalina* is interesting and should be further explored as it might have implications for the classification of the Dictyonellidae (see below under remarks on the genus *Stylissa*).

**Distribution.** This species is distributed mainly through the Sahul Shelf province and occurs between 3–15 m. It

is also recorded from Adele I, Western Australia, in the adjacent Northwest Australian Shelf province, and found at 59 m depth. It has also been observed in Papua New Guinea (Alvarez unpublished).

**Remarks on the genus *Stylissa*.** *Stylissa* was erected by Hallmann (1914) to receive *Stylotella flabelliformis* Hentschel, 1912, which did not agree with the genus *Stylotella* (currently a junior synonym of *Hymeniacidon*, see Van Soest *et al.* 2002). The genus was later related to *Homaxinella* (Suberitidae) by De Laubenfels (1936) based on the presence of styles and to *Dragmaxia* (Axinellidae) by Hooper & Lévi (1993). Following the revision of Van Soest *et al.* (2002), the genus is now considered an established member of the family Dictyonellidae with at least seven species (Van Soest *et al.* 2008). Of those, only *S. flabelliformis* and *S. carteri* are represented in the present study area. The similarities of these species to other members of the genus are discussed above.

Four additional species from the Indo-Pacific realm are referred to *Stylissa* in this paper after examination of the type material – *Homaxinella acanthelloides* Lévi, 1961 (MNHN LBIM DCL697, Zamboanga, Philippines), *Anletta constricta* Pulitzer-Finali, 1982 (MSNG CE 46930, GBR), *Ptilocaulis flexibilis* Lévi, 1961 (MNHN LBIM DCL416, Nha Trang, Vietnam), and *Phakellia inflexa* Pulitzer-Finali, 1982 (MSNG CE 46931, GBR). Some of these species might be closely related to *S. carteri* (i.e. *S. constricta*, *S. flexibilis*) or to *S. massa* (i.e. *S. acanthelloides* and *S. inflexa*). Proper study of the local populations of those species is necessary to confirm these affinities. As seen above, morphological characters of the species within the genus *Stylissa* are highly overlapping and subject to a high degree of variability. *Phakellia crassistylifera* Dendy, 1905 from the Gulf of Manaar (type specimen not examined) might also belong in *Stylissa* as suggested in Alvarez & Hooper (2009).

The wide distribution of some species of *Stylissa* (i.e. *S. carteri* and *S. massa*) suggests that they might constitute species complexes that could only be detected

using molecular methods. Phylogeographic studies will be extremely useful to determine the real limits of these allegedly widespread species.

As mentioned above, there are remarkable similarities between the type species of *Stylissa* (i.e. *S. flabelliformis*) and species of *Scopalina*. They share the surface features and the grainy appearance of the choanosome (also seen in the dictyonellid genera *Svenzea* and *Liosina*). This relationship is supported by molecular evidence from Alvarez *et al.* (2000) which showed the Caribbean species *Scopalina rutzleri* (Wiedenmayer, 1977) was closely related to *S. flabelliformis* (misidentified as *Ulosa sp.* in that publication) based on partial sequences of the 28S rDNA. *Stylissa flabelliformis* was also found to be closely related to *Axinella* and *Agelas* by Erpenbeek *et al.* (2005). The specimen used in that analysis was re-examined here and it is *S. carteri*.

Based on molecular evidence from different data sets and gene regions (Lafay *et al.* 1992; Chombard *et al.* 1997; Alvarez *et al.* 2000; Borehiellini *et al.* 2004; Erpenbeek *et al.* 2005b, 2006; Holmes *et al.* 2007), *Stylissa carteri* and *S. massa* have been consistently related to species of the genus *Axinella* including *A. arnensis* (Hentschel, 1912), *A. corrugata* (George & Wilson, 1919), *A. damicornis* (Esper, 1794) and *A. verrucosa* (Esper, 1794). This polyphyletic cluster of species is shown as also related to members of the order Agelasida in these studies. It is also important to note that this group of species shares similar classes of chemical compounds (Van Soest & Braekman 1999 and references within), providing additional evidence to support their relationship. These close relationships between species presently in different orders and without any obvious morphological similarities remain unexplained at this stage. Indeed, they challenge the value of the currently accepted characters (both morphological and molecular) for the study of halichondrid sponge phylogenetics.

The evidence presented above indicates that the genus *Stylissa* is not monophyletic, which explains some of the discrepancies of the phylogenetic relationships within the Halichondrida. However, there is currently not enough information from other species of *Stylissa* to test the monophyly of this genus and its position within the classification. Studies using both molecular and morphological characters will be undertaken in the future to explore this hypothesis.

## DISCUSSION

This revision indicates that the family Dictyonellidae is represented in the region under study by a total of eight species belonging to the genera *Acanthella*, *Dictyonella*, *Phakettia*, *Scopalina* and *Stylissa*. Three of these genera (i.e. *Dictyonella*, *Phakettia* and *Scopalina*) and the species they contain were not previously recorded for Australian waters.

Other genera of the Dictyonellidae, such as *Liosina*, *Rhaphoxya*, *Lipastrotethya*, *Tethyspira* and *Svenzea* are not

present in the study region. However, species of *Liosina* (e.g. *L. paradoxa* Thiele, 1899) and *Svenzea* (e.g. *S. devoogdae* Alvarez, Van Soest & Rutzler, 2002) are common in regions adjacent to the study area, such as Indonesia and the GBR.

All the species of Dictyonellidae reported here are not restricted to the region under study and are common throughout northern Australia, including the Northwest Australian Shelf, Sahul Shelf, Northeast Australian shelf (Coral Sea), and other localities in Indonesia. Species of *Acanthella* and *Stylissa* in particular are widely distributed with validated records in several marine provinces of the Indo-Pacific, including the Western Indian Ocean. Characterisation of the populations of these species along their distributional ranges using morphological, morphometric and molecular characters are essential to decide whether they include complexes of cryptic species. As in other species of Axinellidae (e.g. *Axinella arnensis*), species of these dictyonellid genera are characteristically variable with intermediate forms along a large morphological continuum that can be detected only by examination of the taxonomic characters across a large number of specimens.

This revision has established that besides the affinities between *Stylissa*, *Axinella*, and members of Agelasida there are also morphological similarities and limited molecular evidence (Alvarez *et al.* 2000) to relate the type species of *Stylissa* (i.e. *Stylissa flabelliformis*) to species of the genus *Scopalina*. This suggests that the genus *Stylissa* is non-monophyletic and its current allocation within sponge classification is debatable. All this evidence however is currently circumstantial and needs to be confirmed in future studies using an appropriate set of taxa selected specifically to explore such puzzling relationships and answer the question of monophyly of the genus *Stylissa* and of the family Dictyonellidae itself.

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Collection and locality data for material examined in the collections of QM and NTM

QM material

G300143	Lee Point Reef, Lee Point, Darwin, NT, 12°19.0001'S, 130°53'E, intertidal, 26 Oct 1984, coll. Hooper, JNA
G300174	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 10.5 m, 3 Apr 1986, coll. Hooper, JNA
G300180	Passage West I., outer reef, Ashmore Reef, WA, 12°14'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Hooper, JNA
G300183	Ashmore Reef, outside entrance to west islet passage, outer reef edge, WA, 12°15'S, 122°55.01'E, 16.5 m, 28 Jul 1986, coll. Hooper, JNA
G300220	Dudley Point Reef, East Point, Darwin, NT, 12°30'S, 130°48.01'E, .5 m, 10 Sep 1987, coll. Hooper, JNA
G300750	Gugari Rip 100 m NE, E Guluwuru I, Wessel Is, NT, 11°34.0001'S, 136°22.12'E, 8 m, 13 Nov 1990, coll. NCI, Australian Institute of Marine Science
G301051	Cartier I, windward reef slope, W side of reef, WA, 12°32.0334'S, 123°31.16'E, 12 m, 4 May 1992, coll. Hooper, JNA
G301053	Cartier I, windward reef slope, W side of reef, WA, 12°32.0334'S, 123°31.16'E, 12 m, 4 May 1992, coll. Hooper, JNA
G301081	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 14 m, 6 May 1992, coll. Hooper, JNA
G301082	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 14 m, 6 May 1992, coll. Hooper, JNA
G301091	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 22 m, 7 May 1992, coll. Hooper, JNA
G301094	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 22 m, 7 May 1992, coll. Hooper, JNA
G301138	Hibernia Reef, entrance to lagoon, NE side reef, WA, 11°57.1334'S, 123°22.06'E, 23 m, 10 May 1992, coll. Hooper, JNA
G301152	Hibernia Reef, lagoon patch reef, E side lagoon, WA, 11°58.05'S, 123°22.06'E, 30 m, 11 May 1992, coll. Hooper, JNA
G301155	Hibernia Reef, outer reef slope, N side of reef, WA, 11°58.0167'S, 123°21.04'E, 27 m, 12 May 1992, coll. Hooper, JNA
G303280	South Shell I., reef N of boatramp, East Arm, Darwin Harbour, NT, 12°29.1334'S, 130°53.09'E, 0 m, 19 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303338	East Point Bommies, Darwin Harbour, NT, 12°24.0834'S, 130°48.14'E, 10 m, 23 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303366	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303386	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303391	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303402	South Shell I., rock on N side of island, Darwin Harbour, NT, 12°29.1334'S, 130°52.16'E, 14 m, 25 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303449	Fish Reef, west side, Bynoe Harbour, NT, 12°26.0167'S, 130°26.09'E, 11 m, 26 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303489	Duyfken Point, W Gulf of Carpentaria, QLD, 12°30.0167'S, 141°2.04'E, 50 m, 4 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303494	Duyfken Point, W Gulf of Carpentaria, QLD, 12°31.0167'S, 141°2.07'E, 51 m, 5 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303495	Duyfken Point, W Gulf of Carpentaria, QLD, 12°31.0167'S, 141°2.07'E, 51 m, 5 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303506	Duyfken Point, W, Weipa, QLD, 12°27.0167'S, 141°3.12'E, 53 m, 6 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303512	Duyfken Point, W, Weipa, QLD, 12°27.0167'S, 141°3.12'E, 53 m, 6 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G304789	N coast, N Jais Aben, off Rewo Village small I., Papua New Guinea, 8°8.0667'S, 145°48.04'E, 2 m, 11 Nov 1993, coll. NCI, Coral Reef Research Foundation
G304937	Duyfken Point, W Gulf of Carpentaria, QLD, 12°25.15'S, 141°4.09'E, 48 m, 3 Mar 1995, coll. Cook, SD. on CSIRO RV Southern Surveyor
G304941	Duyfken Point, W, Weipa, QLD, 12°27.0167'S, 141°3.12'E, 50 m, 3 Mar 1995, coll. Cook, SD. on CSIRO RV Southern Surveyor
G310143	Pary Shoals 35 nm W Bathurst I., NT, 11°6.9001'S, 129°25.51'E, 20 m, 13 Aug 1987, coll. Thom, B. and Locker, R
G311853	Small island 0.5 nm NW of Mainland, N Cape Wilberforce, Melville Bay, Govc, NT, 11°31.5667'S, 136°19.98'E, 20 m, 11 Nov 1990, coll. NT Fisheries
G311872	100 m NE Gugari Rip, East side Guluwuru Is., Wessel Is, NT, 11°20.4'S, 136°13.63'E, 8 m, 13 Nov 1990, coll. Hooper, JNA
G312921	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.0501'S, 148°10.14'E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G312925	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.0501'S, 148°10.14'E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G312938	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.0501'S, 148°10.14'E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G315920	Lagoon entrance, Osprey Reef, Coral Sea, QLD, 13°53.137'S, 146°33.54'E, 20.5 m, 13 Dec 1999, coll. Kennedy, JA and Edson, DW
G316834	Torres Strait, QLD, 9°18.6'S, 142°55.2'E, 11 m, 23 Jan 2004, coll. QDPI RV Gwendoline May

## APPENDIX

Collection and locality data for material examined in the collections of QM and NTM  
NTM material

Z.37	Trepang Bay, Cobourge Peninsula, NT, 11°7'S, 131°58.01'E, 15 Oct 1981, coll. Hooper, JNA
Z.87	Coral Bay, Port Essington, Cobourge Peninsula, NT, 11°11.5001'S, 132°2'E, 18 Oct 1981, coll. Hooper, JNA and Alderslade, PN
Z.187	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0-0.5 m, 13 Sep 1981, coll. Hooper, JNA and party
Z.188	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0-0.5 m, 13 Sep 1981, coll. Hooper, JNA and party
Z.189	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0-0.5 m, 13 Sep 1981, coll. Hooper, JNA and party
Z.272	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0.3 m, 17 Sep 1981, coll. Hooper, JNA
Z.286	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 1 m, 18 Sep 1981, coll. Hooper, JNA and Murray, P
Z.421	Lee Point, Darwin, NT, 12°19.0167'S, 130°53'E, 13 Dec 1981, coll. Hooper, JNA
Z.429	Lee Point, Darwin, NT, 12°19.0167'S, 130°53'E, 13 Dec 1981, coll. Hooper, JNA
Z.433	Lee Point, Darwin, NT, 12°19.0167'S, 130°53'E, 13 Dec 1981, coll. Hooper, JNA
Z.607	Cootamundra Shoals, North of Melville I., NT, 10°49.0667'S, 129°12.09'E, 36 m, 6 May 1982, coll. Thom, B and Lockyer, R
Z.616	Cootamundra Shoals, North of Melville I., NT, 10°50.2167'S, 129°13.17'E, 22 m, 10 May 1982, coll. Lockyer, R
Z.629	Unnamed shoal N Melville I, NT, 11°33'S, 130°3.01'E, 18 m, 25 May 1982, coll. Lockyer, R., Cootamundra Shoals Survey
Z.713	N Adele I., Collier Bay, NW Shelf, WA, 15°58.0167'S, 122°39.07'E, 59 m, 21 Apr 1982, coll. CSIRO R.V.SPRIGHTLY
Z.718	N Adele I., Collier Bay, NW Shelf, WA, 15°58.0167'S, 122°39.07'E, 59 m, 21 Apr 1982, coll. CSIRO R.V.SPRIGHTLY
Z.817	Channel I., Middle Arm, Darwin, NT, 12°32.0167'S, 130°51.02'E, 11 m, 16 Jul 1982, coll. SCOTT CHIDGEY (CALDWELL CONNELL ASS)
Z.862	Channel I., Middle Arm, Darwin, NT, 12°32.0667'S, 130°52.04'E, 13 m, 20 Aug 1982, coll. Alderslade, PN
Z.961	East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA
Z.1447	Blue Hole, Gunn Point, NT, 12°9.0001'S, 131°0'E, 25 m, 19 Aug 1983, coll. Alderslade, PN
Z.1968	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, 11 May 1984, coll. Hooper, JNA and party
Z.2021	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, 11 May 1984, coll. Hooper, JNA and party
Z.2047	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 10 May 1984, coll. Hooper, JNA
Z.2092	northern tip of Weed Reef, outer reef slope, Darwin Harbour, NT, 12°29.2001'S, 130°37.61'E, 23 Aug 1984, coll. Hooper, JNA
Z.2146	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 27 Sep 1984, coll. Hooper, JNA
Z.2155	northern tip of Weed Reef, outer reef slope, Darwin Harbour, NT, 12°29.2001'S, 130°37.61'E, 5 Oct 1984, coll. Hooper, JNA
Z.2192	northern tip of Weed Reef, outer reef slope, Darwin Harbour, NT, 12°29.2001'S, 130°37.61'E, 16 Nov 1984, coll. Hooper, JNA
Z.2251	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 10 12 Apr 1985, coll. Hood, C and party
Z.2321	NW Lacepede Is, NW Shelf, WA, 16°31.0001'S, 121°28.01'E, 38-40 m, 17 Apr 1985, coll. Russell, BC
Z.2351	NW Lacepede Is, NW Shelf, WA, 16°34'S, 121°27.01'E, 40-46 m, 17 Apr 1985, coll. Russell, BC
Z.2379	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 8 m, 29 Jul 1985, coll. Hooper, JNA
Z.2533	Orontes Reef, mouth of Port Essington, Cobourge Peninsula, NT, 11°3.6001'S, 132°5.41'E, 17 Sep 1985, coll. Hooper, JNA
Z.2560	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 12 Dec 1985, coll. Mussig, AM and Hood, C
Z.2633	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2654	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2706	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2710	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2720	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2751	Lagoon, NE west islet, Ashmore Reef, WA, 12°14.4'S, 122°58.89'E, 14 m, 22 Jul 1986, coll. Johnson, C
Z.2774	Channel into lagoon, NW entrance, Ashmore Reef, WA, 12°13.4'S, 122°59'E, 26 Jul 1986, coll. Vail, L
Z.2793	Ashmore Reef, near entrance W islet passage, outer reef edge, WA, 12°14.3'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Mussig, AM
Z.2797	Ashmore Reef, near entrance W islet passage, outer reef edge, WA, 12°14.3'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Mussig, AM
Z.2798	Ashmore Reef, near entrance W islet passage, outer reef edge, WA, 12°14.3'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Mussig, AM
Z.3063	Parry Shoals, Arafura Sea, NT, 11°11.7167'S, 129°43.25'E, 16 m, 12 Aug 1987, coll. Mussig, AM and NCI team

# APPENDIX

Collection and locality data for material examined in the collections of QM and NTM

## NTM material

Z.3081	Parry Shoals, Arafura Sea, NT, 11°11.4'S, 129°43.01'E, 18 m, 13 Aug 1987, coll. Mussig, AM and NCI team
Z.3126	Parry Shoals, Arafura Sea, NT, 11°12'S, 129°43.01'E, 16 m, 12 Aug 1987, coll. Mussig, A.M. and NCI (AIMS)
Z.3199	East Point Reef, East Point, Darwin, NT, 12°29.5'S, 130°48.01'E, 10 m, 17 Sep 1987, coll. Smit, N
Z.3572	Horseshoe Reef, Outer Barrier Reef, Papua New Guinea, 9°40.0001'S, 147°30'E, 18-24 m, 21 Jun 1988, coll. Cook, SD on CSIRO RV Southern Surveyor
Z.3914	NE tip Wigram I., English Company Is, Gove Peninsula, NT, 11°44.3834'S, 136°37.79'E, 20 m, 12 Nov 1990, coll. Hooper, JNA
Z.3924	Cumberland Strait, northern bay, Wessel Is, Gove Peninsula, NT, 11°27.5'S, 136°28.8'E, 20 m, 14 Nov 1990, coll. Hooper, JNA
Z.3926	Cumberland Strait, northern bay, Wessel Is, Gove Peninsula, NT, 11°27.5'S, 136°28.8'E, 20 m, 14 Nov 1990, coll. Hooper, JNA
Z.3954	N side Pugh Shoal, reef slope, NE Truant I., English Company Is., Gove Peninsula, NT, 11°36.5667'S, 136°53.39'E, 20 m, 18 Nov 1990, coll. Hooper, JNA
Z.3960	N side Pugh Shoal, reef slope, NE Truant I., English Company Is., Gove Peninsula, NT, 11°36.5667'S, 136°53.39'E, 18 m, 18 Nov 1990, coll. Hooper, JNA
Z.4456	Iron Ore Wharf, 100 m E Fort Hill Wharf, Darwin Harbour, NT, 12°28.34'S, 130°50.58'E, 5-15 m, 17 Aug 2002, coll. Alvarez, B and party
Z.4461	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 3-7 m, 25 May 2003, coll. Alvarez, B and party
Z.4487	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5 m, 1 Jun 2005, coll. Alvarez, B
Z.4489	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5 m, 1 Jun 2005, coll. Alvarez, B
Z.4493	Bawaka I. near Port Bradshaw, Eastern Arnhem Land, NT, 12°35.206S, 136°46.327E, 12-14 m, coll. Wolf, C
Z.5165	Wickham Point, 2.5 km SW of East Arm Wharf, East Arm, Darwin Harbour, NT, 12°30.12'S, 130°52.39'E, 4-7 m, 15 Sep 2002, coll. Alvarez, B and party
Z.5166	Spencer Point, Indian I., Bynoe Harbour, NT, 12°35.465'S, 130°31.257'E, 6-12 m, 10 Jun 2003, coll. Nguyen, H
Z.5167	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.600'S, 136°17.839'E, 17-20 m, 30 Mar 2004, coll. Alvarez, B
Z.5168	Plater Rock, 1 km E Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 5-16 m, 21 May 2002, coll. Alvarez, B and party
Z.5169	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5-10 m, 26 May 2003, coll. Alvarez, B and party
Z.5170	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.600'S, 136°17.839'E, 17-20 m, 30 Mar 2004, coll. Alvarez, B
Z.5171	Thumb Point, Trafalgar Bay, Marchinbar I., Wessel Is, eastern Arnhem Land, NT, 11°06.690'S, 136°41.262'E, 9-12 m, 31 Mar 2004, coll. Alvarez, B
Z.5172	Rimbija I., 2.8 km W of Cape Wessel, Wessel Is, eastern Arnhem Land, NT, 11°00.208'S, 136°43.836'E, 17-20 m, 1 Apr 2004, coll. Alvarez, B
Z.5173	Plater Rock, 1 km E Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 6-14 m, 22 May 2002, coll. Alvarez, B and party
Z.5174	South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 4-11 m, 18 Aug 2002, coll. Alvarez, B and party
Z.5175	Plater Rock, 1 km E Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 3-12 m, 5 Jun 2002, coll. Alvarez, B and party
Z.5176	Channel Island, 100-400 m N bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, 4-8 m, 7 Jun 2002, coll. Alvarez, B and party
Z.5178	Spencer Point, Indian I., Bynoe Harbour, NT, 12°35.465'S, 130°31.257'E, 6-12 m, 10 Jun 2003, coll. Alvarez, B and party
Z.5179	Angler Reef, approx. 3.5 km NW of Lee Pt, Beagle Gulf, NT, 12°18.78'S, 130°54.03'E, 10-12 m, 1 Sep 2002, coll. Alvarez, B and party
Z.5180	Raft Point, Bynoe Harbour, NT, 12°37.682'S, 130°32.175'E, 5-8 m, 26 Jun 2003, coll. Alvarez, B
Z.5182	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5-10 m, 26 May 2003, coll. Alvarez, B and party
Z.5183	Wigram I., The English Company Is, eastern Arnhem Land, NT, 11°45.822'S, 136°31.900'E, 13-16 m, 29 Mar 2004, coll. Colin, P
Z.5184	off Dudley Point, Fannie Bay, Darwin Harbour, NT, 12°24.96'S, 130°48.83'E, 4-7 m, 4 Jun 2002, coll. Alvarez, B and party
Z.5694	Channel I., Middle Arm, Darwin, NT, 12°32.0667'S, 130°52.04'E, 13 m depth, 20 August 1982, coll. Alderslade, PN
Z.5856	'Bottle Washer' artificial reef, approx. 5 km NW Lee Pt, Beagle Gulf, NT, 12°18.14'S, 130°51.75'E, 8-13 m, 2 Sep 2002, coll. Alvarez, B and party
Z.5857	Channel Island, 100-400 m N bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, intertidal not exposed m, 6 May 2002, coll. Alvarez, B and party

## APPENDIX

Collection and locality data for material examined in the collections of QM and NTM  
**NTM material**

Z.5858	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 6 m, 27 Apr 2007, coll. Alvarez, B
Z.5861	N Edgell, off Kota Kinabalu, Malaysia, 6°00.629'N, 115°59.382'E, 10-28 m, 23 Oct 2005, coll. Alvarez, B
Z.5862	N Gaya I., off Kota Kinabalu, Malaysia, 6°02.068'N, 116°00.385'E, 10-18 m, 23 Oct 2005, coll. Alvarez, B
Z.5865	Plater Rock, 1 km E Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 5-16 m, 21 May 2002, coll. Alvarez, B and party
Z.5866	S Edgell, Kota Kinabalu, Malaysia, 6°00.259'N, 115°59.169'E, 10-20 m, 25 Oct 2005, coll. Alvarez, B
Z.5867	S Edgell, Kota Kinabalu, Malaysia, 6°00.259'N, 115°59.169'E, 10-20 m, 25 Oct 2005, coll. Alvarez, B
Z.5868	S Gaya I., Kota Kinabalu, Malaysia, 6°00.403'N, 116°01.572'E, 10-12 m, 25 Oct 2005, coll. Colin, P
Z.5870	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 10 m, 8 May 2006, coll. Alvarez, B
Z.5871	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.2001'S, 130°47.1'E, 5-19 m, 8 May 2002, coll. Alvarez, B and party
Z.5882	'Bottle Washer' artificial reef, approx. 5 km NW Lee Pt, Beagle Gulf, NT, 12°18.14'S, 130°51.75'E, 8-13 m, 2 Sep 2002, coll. Alvarez, B and party
Z.5885	Channel Island, 100-400 m N bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, 4-8 m, 6 May 2002, coll. Alvarez, B and party
Z.5886	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 3-12 m, 1 Jun 2005, coll. Alvarez, B
Z.5896	off Dudley Point, Fannie Bay, Darwin Harbour, NT, 12°24.96'S, 130°48.83'E, 4-7 m, 4 Jun 2002, coll. Alvarez, B and party